STUDIES IN THE MILLIPED ORDER CHORDEUMIDA (DIPLOPODA): A REVISION OF THE FAMILY CLEIDOGONIDAE AND A RECLASSIFICATION OF THE ORDER CHORDEUMIDA IN THE NEW WORLD

WILLIAM A. SHEAR[1]

TABLE OF CONTENTS

ABSTRACT. This study of North American chordeumid millipeds is in two parts: a revision of the large family Cleidogonidae and a reclassification of the Order Chordeumida in the New World. In part one, the zoogeography and possible evolution of the Cleidogonidae are discussed. The family probably originated in the highlands of central and southern Mexico and subsequently spread north and south, enduring several waves of extinction that left behind numerous peculiar relict forms. The family names Dybasiidae Loomis, Bactropidae Chamberlin and Hoffman, and Bactropodellidae Jeekel are considered here as synonyms of Cleidogonidae Cook for the first time. *Dearolfia* Loomis is placed in the synonymy

---

[1] Department of Biology, Concord College, Athens, West Virginia 24712.

of *Pseudotremia* Cope; *Mexiceuma* Verhoeff, *Rhabdarona* Chamberlin and Mulaik, *Cavota* Chamberlin, *Hirsutogona* Kraus, *Mecistopus* Loomis, *Acakandra* Loomis, and *Costaricia* Loomis are placed in the synonymy of *Cleidogona* Cook; *Bactropus* Cook and Collins (preoccupied), *Bactropodellus* Jeekel, *Ofcookogona* Causey and *Ozarkogona* Causey are synonyms of *Tiganogona* Chamberlin; *Ogkomus* Loomis and *Solemia* Loomis are synonyms of *Dybasia* Loomis.

The following new synonymies at the species level are recognized (valid name given first): *Pseudotremia carterensis* Packard = *P. sodalis* Loomis; *Cleidogona maculata* (Verhoeff) = *C. leona* Chamberlin, *C. propria* Causey; *C. bacillipus* (Chamberlin and Mulaik) = *Mecistopus varicornis* Loomis; *C. celerita* Williams and Hefner = *C. inflata* Causey; *C. caesioannulata* (Wood) = *C. exaspera* Williams and Hefner; *C. laminata* Cook and Collins = *C. aspera* Causey. The following species are described as new: *Pseudotremia stupefactor, P. lethe, P. acheron, P. cocytus, P. cottus, P. soco, P. momus, P. armesi, P. nefanda, P. alecto, P. amphiorax, P. tsuga, P. scrutorum, P. merops, P. spira, P. nyx, P. cercops, P. lictor, P. aeacus, P. unca, P. minos, P. deprehendor, Solaenogona chiapas, Cleidogona accretis, C. fidelitor, C. georgia, C. lachesis, C. hoffmani, C. steno, C. tallapoosa, C. grenada, C. nantahala, C. atropos, C. laquinta, C. conotyloides, C. forficula, C. chontala, C. tizoc, C. xolotl, C. tequila, C. hauatla, C. baroqua, C. crystallina, C. pecki, C. gucumatz, C. mixteca, C. decurva, C. mayapec, C. camazotz, C. chacmool, C. zapoteca, C. totonaca.*

In part two, the known families of New World chordeumids are arranged into superfamilies. Superfamily Striarioidea Cook includes the families Striariidae Cook, Caseyidae Verhoeff, Rhiscosomididae Silvestri, and Urochordeumidae Silvestri; the new superfamily Heterochordeumoidea includes the families Conotylidae Cook and Adritylidae Shear (as well as a few families not found in the New World); the new superfamily Cleidogonoidea includes the families Cleidogonidae Cook and Trichopetalidae Verhoeff; the new superfamily Brannerioidea includes the families Branneriidae Cook and Tingupidae Loomis. The possible relationships of the families are briefly discussed, and useful characters are assessed.

The family Idagonidae Buckett and Gardner is placed for the first time in the synonymy of the family Conotylidae Cook. The genera *Zygonopus* Ryder, *Tynopus* Chamberlin and *Flagellopetalum* Causey are treated as synonyms of *Trichopetalum* Harger. *Tingupa monterea* Chamberlin is transferred to the genus *Rhiscosomides*. The following species are described as new: *Rhiscosomides acovescor, Trichopetalum syntheticum, Scoterpes ventus* and *Mexiterpes metallicus*.

GENERAL INTRODUCTION

The milliped Order Chordeumida is a large assemblage of species belonging to the Subclass Chilognatha and having in common a number of very basic features: the sterna are free from the pleurotergites of the diplosegments, and the pleurotergites are not fused in the middorsal line; the anal segment bears two small spinnerets; segment numbers are constant within species and are either 26, 28, 30, or 32; the mentum of the gnathochilarium separates the lingual laminae and is sometimes divided; repugnatorial glands are absent. Beyond this basic similarity is a bewildering array of adaptive types, ranging from species normally active at or near the freezing point of water, to inhabitants of leaf litter of the tropical rain forest, and from nearly transparent troglobites to heavily armored burrowers. They range in size from 3 mm to nearly 40 mm.

Biological studies on this group (and millipeds in general) have been inhibited by the primitive state of milliped taxonomy. Less than a fourth of the species of millipeds inhabiting the United States have been described, as I judge from my own collecting experiences in several areas. In the past, only a few workers have made any attempt to gather together collections of millipeds and study them in a systematic way. Papers describing a miscellany of new species have been the rule, rather than revisions of genera and families (in the Chordeumida, *only one* revision of a genus, including four species, has appeared since 1895). Since 1955, a few exemplary studies of milliped families, such as R. L. Hoffman's ongoing revision of the very large family Xystodesmidae, and W. T. Keeton's complete study of the Spirobolidae, have appeared. The Order Chordeumida has been neglected.

This present study must be considered incomplete for a number of reasons. First, many additional species of the family Cleidogonidae remain to be discovered, as do additional genera and species of other families briefly treated here. Second, a large collection in private hands, comprising several hundred vials of *Pseudotremia*, was not available for study, and a number of unique types of previously described species have either been lost or never found their way to their published repository.

ACKNOWLEDGMENTS

Dr. Herbert W. Levi of the Museum of Comparative Zoology has my thanks for his help, encouragement, and many kindnesses; he made possible my stay at Harvard and did much to expedite the completion of this study.

Dr. Richard L. Hoffman, Radford College, Radford, Virginia, foremost American authority on the Diplopoda, suggested the topic and provided many of the specimens used. Dr. Hoffman also made many valuable suggestions, and never failed to reply in detail to hastily written queries, despite his overloaded schedule.

Dr. Stewart Peck of the Museum of Comparative Zoology contributed a number of significant specimens, and, in numerous conversations in our shared office, helped clarify my thinking concerning the evolution of cave animals. Dr. Nell B. Causey, Baton Rouge, Louisiana, loaned collections of branneriids and of Mexican cleidogonids. Further specimens were loaned or contributed by Michael R. Gardner, Davis, California; Dr. John Holsinger, Norfolk, Virginia; Dr. Thomas C. Barr and John and Martha Cooper, Lexington, Kentucky; Dr. J. A. Beatty, Carbondale, Ill.; Dr. F. A. Coyle, Cullowhee, N. C.; and, Dr. A. A. Weaver, Wooster, Ohio.

I thank the following museums and their curators for the loan of type specimens, which often involved laborious searching: Museum of Comparative Zoology (Dr. H. W. Levi), American Museum of Natural History (Dr. J. A. L. Cooke), United States National Museum (Dr. Ralph E. Crabill, Jr.), University of Utah Zoology Museum (Mr. T. Lorenz), Illinois Natural History Survey (Dr. John Unzicker), Field Museum of Natural History (Mr. Henry Dybas), Philadelphia Academy of Sciences (Dr. N. Jago), The British Museum (Natural History) (Dr. J. G. Sheals and Mr. D. Clark), Senckenbergische Naturforschende Gesellschaft in Frankfurt (Dr. M. Grasshoff), Muséum d'Histoire Naturelle de Genève (Dr. B. Hauser), Zoologische Museum, Munich (Dr. W. Engelhardt and Dr. E. Popp).

I am also appreciative of the generous financial support of Harvard University, through the Committee on Evolutionary Biology (National Science Foundation Grant GB-7346), and through my tenure as a Richmond Fellow.

A number of friends and colleagues provided help through their hospitality during field studies; in particular Dr. and Mrs. Carl J. Chapman, Dr. and Mrs. Frederick A. Coyle, Dr. and Mrs. Jeremiah L. Blatt, and Mr. and Mrs. David R. Bard. The encouragement of the faculty and students of the Biology Department of Concord College, Athens, West Virginia, was also appreciated. Dr. Peter J. van Helsdingen helped with a number of tasks involved in completing the manuscript, and Prof. Frank Carpenter made several valuable suggestions.

The manuscript was typed by Wilmoth Peairs and Mrs. Sally Loth, who cheerfully put up with the hurriedly delivered fragments of typescript and constant changes and harassment.

Part I. A Revision of the Family Cleidogonidae

INTRODUCTION

Before the higher classification of any group of animals or plants can be established, thorough studies of the species, genera, and families involved are necessary. Such studies, as previously stated, have generally been lacking with regard to millipeds. In the Chordeumida, progress in studying the evolutionary relationships of the various forms has been hampered by the presence of several poorly known small families and a single large one, the Cleidogonidae, in which less than half the species have been described. Some of these smaller families are handled in more or less detail in the second part of this paper, and a moderate-sized family, the Conotylidae, has already been revised (Shear, 1971). The first section of this paper removes another of the obstacles listed above by revising the large family Cleidogonidae.

Because most of the species in the family Cleidogonidae remained undescribed, taxonomists having only a nodding acquaintance with the group set up numbers of superfluous genera and families (Verhoeff, 1936; Chamberlin and Hoffman, 1958; Kraus, 1954; Loomis, 1964, 1966; Causey, 1951b; etc., etc.). In the course of this study, intermediate species and genera were discovered that make most of these names obsolete.

Species of the family Cleidogonidae are among the commonest millipeds in two crucial biogeographic areas: the central Appalachian Mountains of North America and the highlands of Mexico. In both these areas, rapid and probably recent speciation in the genera *Cleidogona* and *Pseudotremia* have produced a confusing picture of highly localized distributions. Much work remains to be done in discovering the distributional details of most of the species. When this has been accomplished, perhaps the number of species can be reduced; something of this kind has been necessary in this paper, though the discovery of new species has completely swamped the relatively small number of names placed in synonymy. In addition, some peculiar patterns are emerging. Along with highly localized species, there are others that, although seemingly not very different, are widely distributed. This problem is discussed in more detail later.

Little is known about the biology of the Cleidogonidae, and what additional information I have uncovered is treated both under the species involved, and, as it bears on collecting methods, in the section METHODS AND MATERIALS below.

METHODS AND MATERIALS

Approximately 2500 specimens of members of the family Cleidogonidae were examined during the course of this study. All were preserved in 70–85 percent ethanol. The majority of specimens came from the personal collections of Drs. Richard L. Hoffman and Nell B. Causey, and have been returned to them, with the exception of types of new species, all of which have been deposited in the Museum of Comparative Zoology. Nearly 200 specimens were taken by me in collecting seasons from 1962–1967 in Ohio, West Virginia, Virginia, and in Tennessee, North Carolina, Georgia and South Carolina during the collecting season of 1969. Some of these specimens, with the exception of types, are retained by me for the time being.

Collecting methods. Two collecting methods proved most successful in the search for cleidogonids. Since most epigean species are dwellers in leaf-litter, scraping away the dry upper layer and sorting the moist, rotting duff underneath yielded many specimens. Tullgren funnel sampling was also successful, especially in collecting quantities of specimens of smaller species.

Hypogean species of *Pseudotremia* must be searched for in caves, where, in most instances, they are found on the floor, regardless of lighting conditions. The most important factor seems to be the presence of washed-in food, usually wood or other vegetable debris. Troglophilic species are frequently common in cave entrances. At Laurel Creek Cave, Greenville, West Virginia, a good sample of *Pseudotremia hobbsi* was taken beneath rocks and logs at the cave mouth where water dripped from the cliff above.

Some *Cleidogona* have a definite preference for dry conditions. For example, six adult males of *C. fustis* were taken at Athens, West Virginia, under stones in a sloping, south-facing pasture. *Cleidogona major* is common on West Virginia shale barrens, in a very warm and dry microclimate.

Upland oak forests and cove forests are the most productive Appalachian habitats for *Cleidogona;* coniferous forests in general support few millipeds. However, *Pseudotremia* is frequently taken in association with hemlock (*Tsuga canadensis*) or fir (*Abies fraseri*). On one occasion, two immature *Cleidogona* were collected in a fir forest near the summit of Mt. Mitchell, North Carolina.

The best collecting conditions occur from late March to early June, and again in October and November, depending on the latitude. Most individuals probably either estivate or burrow deeper into the soil and litter during the hot, dry summer months.

In Mexico species are commonly found in caves, and at somewhat higher altitudes than is usual in the United States. Some species have been collected in central Mexico as high as 14,000 feet (*ca.* 4500 m), but others may occur on the coastal plains. Again, broadleaf forests are most productive, particularly the so-called cloud forest.

Living specimens, especially of *Cleidogona,* are fragile and do not transport well. Unless they are specifically required in living condition, it is best to kill and preserve them in 70–85 percent ethanol in the field. Specimens preserved in the lower concentrations of alcohol remain more flexible.

Dissecting methods. It is rarely possible to make adequate observations on the genitalia of the cleidogonids without dissection. This should be done with least damage to the specimen. I have found the following procedure useful. For tightly coiled males, it is usually necessary to break the body into two parts. This is best done with a pair of watchmaker's forceps between the seventh and eighth segments. The anterior and posterior gonopods will be exposed on one of the broken surfaces, and the tenth and eleventh legs on the other. The break can be made to occur neatly between the segments if gentle pressure and careful sawing movements of the forceps are used, so as to cut the muscles and do a minimum amount of damage to the cuticle. Next, the muscles attaching the tracheal apodemes of the gonopods to the body wall and to the preceding pair of legs should be severed by the use of a microscalpel made from a chip of razor blade. The gonopods can now be removed from the body with forceps or needles. Particular care must be taken to avoid damaging the anterior basal region during this part of the dissection. The anterior and posterior gonopods can be separated by using two needles to apply pressure gently in opposite directions, first at one lateral sternal angle, then at the other. Damage results when the separation is attempted from the middle of the sternum, owing to the weakness of this structure in the posterior gonopods.

Cleaning the muscular tissue from the anterior gonopods is sometimes useful. A number of methods involving corrosives or enzymes have been successful: soaking for twelve hours in cold 10 percent potassium hydroxide; one hour in saturated hydrogen peroxide; soaking twelve hours in a solution of the proteolytic enzyme trypsin at 90–95°F (40°C). The latter method is preferred because it results in less distortion to the sclerotized parts.

Dissection of the female cyphopods is somewhat more difficult. These structures are located posterior to the coxae of the second legs. The best procedure seems to be to separate the head and collum from the rest of the body, then remove the second and third legs as a unit from the second thoracic segment. The third legs can then be carefully pried away from the cyphopods and second legs. Care must be taken to avoid damaging the postgenital plate, present immediately behind the cyphopods in most species of *Cleidogona.* It is rarely necessary to clean muscular tissue from the cyphopods, but if the need arises, the same methods can be used as mentioned above for the gonopods.

Many specimens had important morphological characters obscured by dirt, material from the digestive tract, or chemical deposits resulting from improper preservation. Cleaning this material, particularly from the delicate gonopods, with brushes and needles, may cause damage. Ultrasonic cleaning, however, removed almost every kind of debris in a few moments without damage to the most fragile structures (Shear and Levi, 1970). The machine used was a DiSon System 30 Ultrasonic generator, manufactured by Ultrasonic Industries, Engineer Hill, New York. Specimens to be cleaned were placed in a 17 × 60 mm glass vial of alcohol and immersed in the cleaning bath for from one to five minutes.

Illustrations. Illustrations were prepared at various magnifications, depending on the size of the structure to be drawn. Scale is clearly indicated for all illustrations. Drawings were first made in pencil with the use of ruled paper and an ocular grid; most were checked for details under higher magnification before being transferred in ink to heavier drawing paper. Measurements were made with an ocular micrometer and are accurate to 0.01 mm.

Family Cleidogonidae Cook, 1896

Cleidogonidae Cook, 1896, Brandtia, 2: 8; Hoffman, 1950, J. Washington Acad. Sci., 40: 87 (key to genera, list of species); Chamberlin and Hoffman, 1858, Bull. U. S. Nat. Mus., 212: 89 (list of U. S. genera and species); Loomis, 1968, U. S. Nat. Mus. Bull., 266: 66 (list of Mexican and Central American species).

Entomobielziinae Verhoeff, 1909, Zool. Anz., 34: 570 (in part, not including *Entomobielzia* Verhoeff).

Mexiceumidae Verhoeff, 1926, Zool. Anz., 68: 110.

Pseudocleididae Attems, 1926, *in* Kükenthal-Krumbach, Handbuch der Zoologie, 4: 170 (in part, not including *Pseudoclis* Attems).

Bactropidae Chamberlin and Hoffman, 1950, Chicago Acad. Sci. Nat. Hist. Miscellany, 71: 6. NEW SUBJECTIVE SYNONYMY.

Dybasiidae Loomis, 1964, Fieldiana, 47: 100. NEW SUBJECTIVE SYNONYMY.

Bactropodellidae Jeekel, 1969, Entomol. Bericht., 29: 88. New name for Bactropidae. NEW SUBJECTIVE SYNONYMY.

Type genera. Of Cleidogonidae, *Cleidogona* Cook and Collins, 1895; of Bactropidae, *Bactropus* Cook and Collins, 1895; of Mexiceumidae, *Mexiceuma* Verhoeff, 1926; of Dybasiidae, *Dybasia* Loomis, 1964.

Notes on synonymy. The Entomobielziinae of Verhoeff and Attems' Pseudocleididae were erected on European genera that superficially resemble cleidogonids, and those authors probably included the American genera for that reason, apparently not concerned that by doing so they were bringing Cook's earlier family name into the problem. *Mexiceuma* is a junior subjective synonym of *Cleidogona.* The family Bactropidae was based on the genus *Bactropus* by Chamberlin and Hoffman, because Cook and Collins (1895) stated in the original description that the promentum was "not distinct." Chamberlin and Hoffman (1950) took this to mean that the promentum was absent. The holotype of *B. conifer* was not examined by them or me and is presumed to be lost. However, a number of other species actually belonging to this genus have been described under a variety of generic names, and all have a separate promentum. The original meaning of Cook and Collins' statement was probably that the promentum was difficult to see on the small holotype of *Bactropus conifer*. In any case, the generic name is preoccupied by *Bactropus* Barrande, 1872, a fossil crustacean of uncertain taxonomic position. The genera and species placed by Loomis in the family Dybasiidae do not differ in any important character from species of the Cleidogonidae, and indeed are related much more closely to *Cleidogona* than other genera traditionally placed in the Cleidogonidae.

Diagnosis. See the key to North American chordeumid families given in the second part of this paper.

Description. Thirty segments. Mentum divided. Antennae long to moderately short. Ocelli present, though in many cases reduced in number and depigmented. Body tapering gradually at either end, but more abruptly anteriorly in males, widest in males at seventh segment. Body segments smooth, cylindrical, or with pronounced thick shoulders, or with *Conotyla*-like paranota; in one genus (*Pseudotremia*) with coarse knobs or rugae dorsally and with lateral striations. Segmental setae present, prominent, or small and spatulate. Pregonopodal legs of males: legs 1 and 2 of normal size or slightly smaller, 6-segmented. Legs 3 through 7 enlarged, crassate, 7-segmented. Anterior gonopods: sternum usually well sclerotized, lateral sternal sclerites more or less set off by suture in region of spiracle. Coxae separate or fused, usually with setae. Colpocoxites fused to coxae or separated by a suture, with 1 or 2 branches; if 2, then lateral branch with a gland channel. Telopodites simple, much reduced. 1-segmented or absent, fused to each other, but sometimes movable with respect to coxae. Posterior gonopods: without colpocoxites, coxae always largest segments, 2- to 6-segmented, claw present in all but a few species. Tenth and eleventh legs with coxal glands, frequently with other modifications on the coxae that may be constant or variable within genera. Twelfth sternum with or without an anterior projection. Following legs unmodified. Cyphopods: receptacle large (*Pseudotremia*) or reduced in size (*Cleidogona*); two pairs of postreceptacular bars. Valves well sclerotized, sometimes (*Cleidogona*) with ornate modifications. Postgenital plate present in *Cleidogona* and *Solaenogona*.

Distribution. Panama, Costa Rica, El Salvador, Guatemala, southern and eastern Mexico, southern Texas, United States east of the Mississippi River and south of the Great Lakes.

Species Not Included in the Revision

The following species could not be included in the revision because, for one reason or another, it was impossible to study the type material, the only known specimens.

Types of the following species could not be located at the published repository, the American Museum of Natural History:

Cleidogona saripa Causey

Cleidogona saripa Causey, 1961, Florida Entomol. 44: 36, figs. 1, 2, ♂. Male holotype from Savannah River Plant, Aiken Co., South Carolina.

Cleidogona arkansana Causey

Cleidogona arkansana Causey, 1954, Tulane Stud. Zool., 2: 66, figs. 6–9, ♂. Male holotype from 4 mi. east of Princeton, Dallas Co., Arkansas. Probably a synonym of *C. unita* Causey.

Cleidogona moderata Causey

Cleidogona moderata Causey, 1957, J. Kansas Entomol. Soc., 30: 115, figs. 6, 7, ♂. Male holotype from 18 mi. south of Tamazunchale, San Luis Potosí, Mexico. A member of the *maculata*-group of *Cleidogona*.

Cleidogona secreta Causey

Cleidogona secreta Causey, 1957, J. Kansas Entomol. Soc., 30: 119, fig. 16, ♀. Female holotype from Oaxaca City, Oaxaca, Mexico.

Tiganogona levis (Causey) NEW COMBINATION

Ozarkogona levis Causey, 1959, J. Kansas Entomol. Soc., 32: 143, figs. 1, 2, ♂. Male holotype from Richmond Creek, Greene Co., Indiana. Probably a synonym of *Tiganogona conifer* (Cook and Collins).

Tiganogona ladymani (Causey) NEW COMBINATION

Ozarkogona ladymani Causey, Proc. Biol. Soc. Washington, 65: 114, figs. 8, 9, ♂. Male holotype from Rector, Clay Co., Arkansas.

Types of the following species could not be located at the published repository, the United States National Museum.

Cleidogona forceps Cook and Collins

Cleidogona forceps Cook and Collins, 1895, Ann. New York Acad. Sci., 9: 49, figs. 159, 163, ♂. Type locality not specified, no localities known for this species.

Cleidogona australis Loomis

Cleidogona australis Loomis, 1966, Proc. Biol. Soc. Washington, 79: 226, figs. 8–10, ♂. Male holotype from Highlands Hammock State Park, Sebring, Florida.

Cleidogona curvipes (Loomis) NEW COMBINATION

Costaricia curvipes Loomis, 1966, Proc. Biol. Soc. Washington, 79: 227, figs. 11–13, ♂. Male holotype from Cairo, Limon Prov., Costa Rica.

Tiganogona conifer (Cook and Collins) NEW COMBINATION

Bactropus conifer Cook and Collins, 1895, Ann. New York Acad. Sci., 9: 54, figs. 172–176, ♂. Male holotype from Bloomington, Monroe Co., Indiana.

Types of the following species were sent by the Philadelphia Academy of Science and were apparently lost in the mails:

Tiganogona steuartae (Causey) NEW COMBINATION

Ofcookogona steuartae Causey, 1951, Proc. Biol. Soc. Washington, 64: 121, fig. 13, ♂. Male holotype from Greenwood, Sebastian Co., Arkansas.

Cleidogona minima Causey

Cleidogona minima Causey, 1951, J. Washington Acad. Sci., 41: 80, figs. 10–13, ♂. Male holotype from Tuscaloosa, Tuscaloosa Co., Alabama.

The types of the following species could not be located in the University of Utah collection:

Cleidogona mandeli Chamberlin

Cleidogona mandeli Chamberlin, 1952, Great Basin Natur., 12: 13, figs. 4–7, ♂. Male holotype from Volcán Tajmulco, Guatemala.

Cleidogona punctifer Chamberlin

Cleidogona punctifer Chamberlin, 1952, Great Basin Natur., 12: 13, no figure. Female holotype from Chichivac, Guatemala.

Cleidogona tajmulco Chamberlin

Cleidogona tajmulco Chamberlin, 1952, Great Basin Natur., 12: 15, no figures. Female holotype from Volcán Tajmulco, Guatemala.

Cleidogona zempoala Chamberlin

Cleidogona zempoala Chamberlin, 1943, Bull. Univ. Utah, 34: 35, figs. 64, 65, ♂. Male holotype from Parque Nacional de Zempoala, Morelos, Mexico.

Pseudotremia hansoni Chamberlin

Pseudotremia hansoni Chamberlin, 1951, Great Basin Natur., 11: 25, no figures. Female holotype from Pineville, Kentucky.

Pseudotremia fracta Chamberlin

Pseudotremia fracta Chamberlin, 1951, Great Basin Natur., 11: 25, no figures. Female holotype from Gatlinburg Cove, Gatlinburg, Tennessee. This name might have been used for *P. cottus*, but *P. fracta* as described by Chamberlin seems to be smaller and has only 10 ocelli. Perhaps the female holotype was not mature.

The following species could not be studied in detail because the vials containing the types contained no gonopods:

Cleidogona austrina (Loomis) NEW COMBINATION

Acakandra austrina Loomis, 1964, Fieldiana, 47: 99, figs. 9N–9Q, ♂. Male holotype from Cerro Punta, Chiriquí Prov., Panama, type deposited in Chicago Natural History Museum.

Cleidogona nueva Chamberlin

Cleidogona nueva Chamberlin, 1941, Entomol. News, 52: 250. Male holotype from Ojo de Augua, Sabinas Hidalgo, Nuevo León, Mexico, type deposited in collection of University of Utah. The holotype of the supposed subspecies *C. nueva michoacana,* deposited in the University of Utah collection, also lacked gonopods.

Evolution and Zoogeography of the Genera of Cleidogonidae

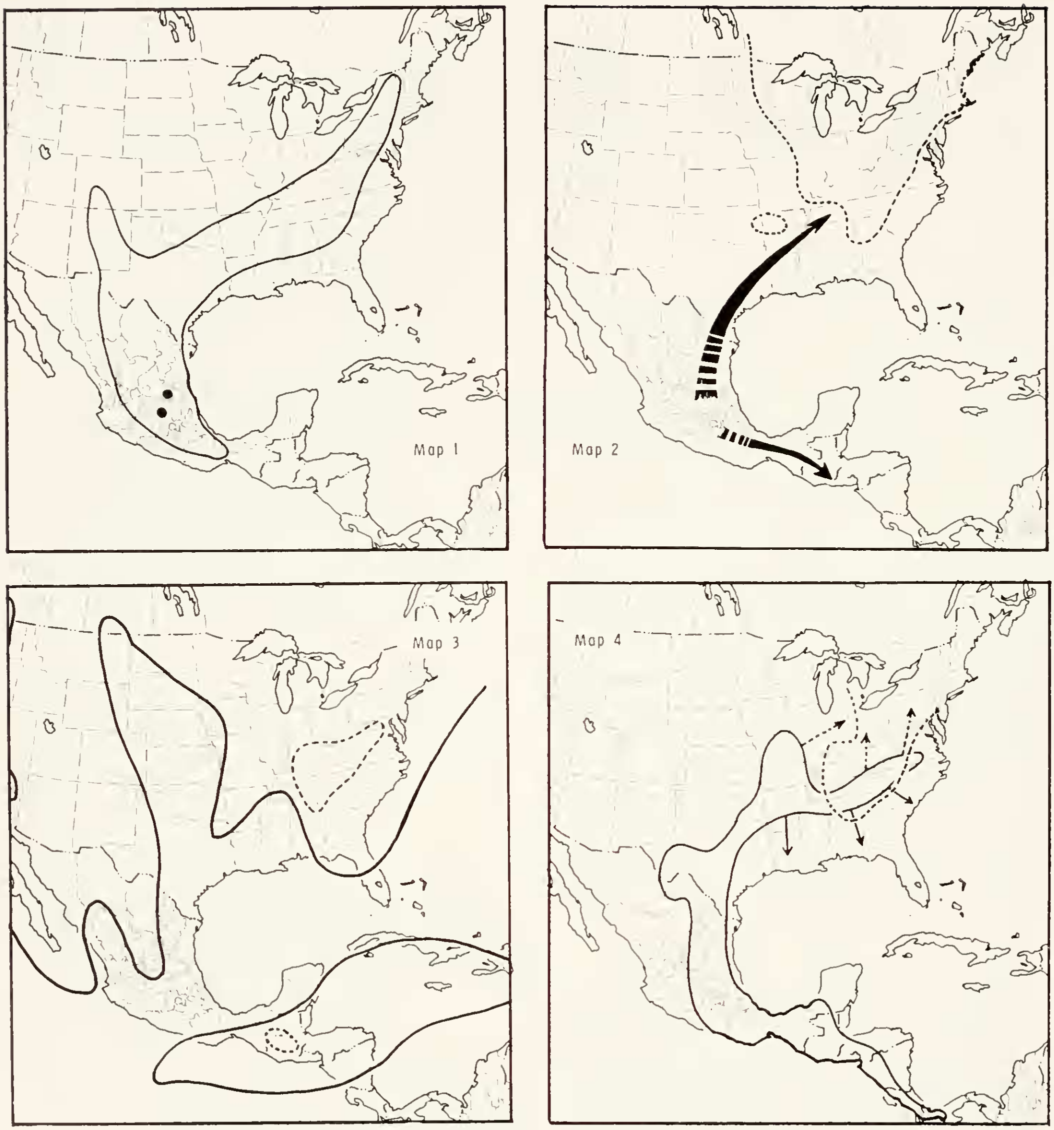
Hoffman (1969a, 1969b) made the first serious attempt in America to bring together information on the evolution and zoogeography of the Diplopoda. He did not include the chordeumids, however, because of the great confusion in their taxonomy. He concluded that with the exception of recent periods of rapid expansion and speciation in certain families, most of the events accounting for the present distribution of milliped orders, and perhaps the origins of the orders themselves, took place as early as the late Paleozoic. The fossil record (summarized in Hoffman, 1969b) is extremely skimpy, but forms not unlike those living today have been found in North American Upper Pennsylvanian sediments. A few forms are known from the Oligocene European Amber; they are members of families and possibly even genera found in Europe today.

Thus any attempt at historical zoogeography in millipeds must be highly speculative and must rely almost entirely on evidence from present distributions and analogies from groups with similar patterns.

In his discussion of other milliped orders, Hoffman (1969a) pointed out that there have been two major American centers of speciation and subsequent range expansion; the highlands of north central Mexico and the southern Appalachian Mountains. A third center may exist in the coastal ranges of the Pacific Northwest; too little is known about the fauna there to make a firm statement. My findings in the Cleidogonidae and other milliped families reinforce Hoffman's conclusions. In the following discussion, I have relied heavily on the information on paleogeography presented by Schuchert (1955) and Maldonado-Koerdell (1964), and the conceptual methods expounded by Darlington (1957, 1965).

In the second part of this paper, I have combined the families Cleidogonidae and Trichopetalidae under the new superfamily Cleidogonoidea; the reader is referred to that section for the evidence for this arrangement. Here I will only state that species of the genus *Mexiterpes* (Trichopetalidae) are quite intermediate in many respects between more typical trichopetalids and *Pseudotremia* (Cleidogonidae). The two families may have developed from a common stock beginning in the early Cretaceous, or even before.

In Map 1 the possible distribution of this early stock is shown. It may have been similar to *Mexiterpes* in many respects (dots show records of two species of *Mexiterpes,* both from caves), but probably had larger, more loosely articulated gonopod telopodites and lacked the obviously derived body form of the trichopetalids. The earliest differentiation of the two families, into a stock more closely resembling *Mexiterpes* and leading to the trichopetalids of North America, and a second line intermediate between *Mexiterpes* and *Pseudotremia,* from which the Cleidogonidae developed, may have taken place in the late Jurassic, when, except for submersion of coastal areas, the extent of the North American land mass was essentially as it is today (Schuchert, 1955). The more progressive proto-*Pseudotremia* stock expanded both northward and southward from an origin in the Mexican highlands, and may have limited the distribution of the early trichopetalids to the northern part of the continent by competition. Map 2 shows (dashed line) the present distribution of the Trichopetalidae in eastern North America. The heavy arrows indicate the possible invasion routes of the proto-*Pseudotremia* stock. The distribution and



Maps 1–4. Speculations on historical zoogeography of the Cleidogonidae and Trichopetalidae. See text for explanations.

isolation of this stock into northern and southern elements took place perhaps during the Cretaceous. Map 3 (after Schuchert, 1955) shows the maximum extent of the seas of Cretaceous time (heavy line), and the present distributions (dashed lines) of the genera *Pseudotremia* and *Solaenogona,* which I believe to be direct derivatives of the early proto-*Pseudotremia* stock. At some time during the Cenozoic, possibly as recently as the Miocene, ancestral *Cleidogona* originated from forms similar to the present-day *Solaenogona.* This very progressive, adaptable genus has since spread both northward and southward, though undoubtedly

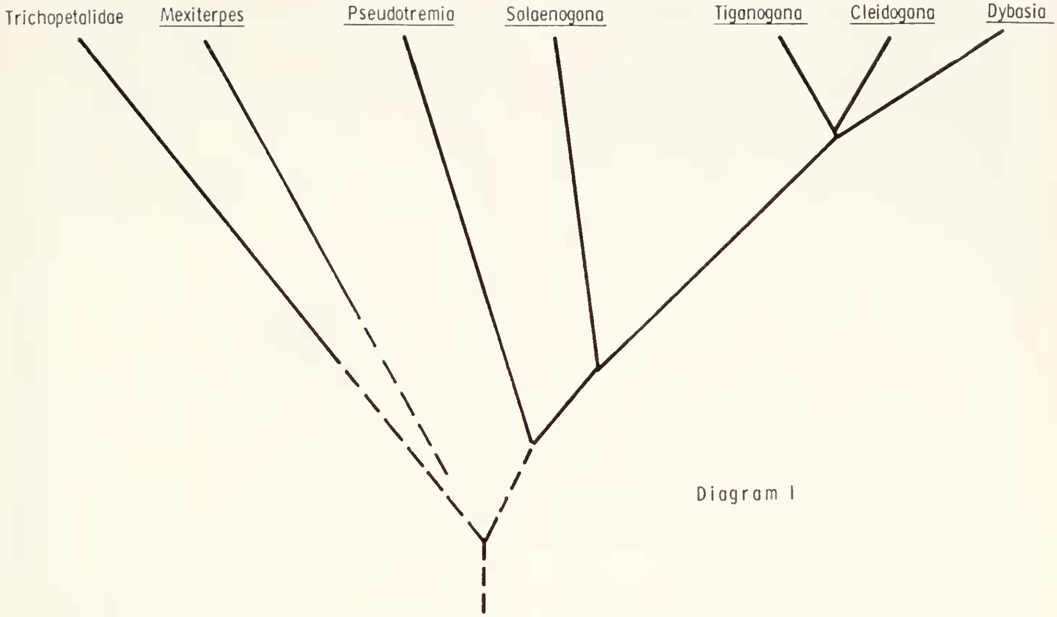


Diagram 1. Suggested phylogeny of genera of Cleidogonidae, showing relationship to the genus *Mexiterpes* and the family Trichopetalidae. Time scale not to be inferred.

there have been many intervening periods of recession and extinction (see the discussion under *Cleidogona*). Map 4 shows the speculative early distribution of *Cleidogona* (heavy line) and its satellite genera, *Tiganogona* and *Dybasia*. Solid arrows indicate movement southward from a secondary center in the southern Appalachians, and dashed arrows northward expansion. The dashed line represents speculation about the distribution of *Pseudotremia* at that time; since then it has been limited drastically from the north (compare Map 5) by glaciation, and by competition from *Cleidogona*.

Tiganogona is a small genus apparently adapted to somewhat drier climatic conditions than *Cleidogona*. It may have developed as a purely North American derivative of early Appalachian *Cleidogona*, or be most closely related to the Mexican species grouped around *C. maculata*. Specimens are rare and species limited in their distributions.

Dybasia occurs in Panama at the extreme southern limit of the distribution of the family. It is clearly a specialized stock of *Cleidogona*, and may not be worthy of generic recognition.

Members of the Cleidogonidae make up a predominately austral element of the North American milliped fauna, with some species of *Cleidogona* and members of the genus *Pseudotremia* secondarily adapted to boreal conditions. On the other hand, the family Trichopetalidae is distinctly boreal, with many species in the northern sections of North America adapted to activity in the winter. Other species are widespread in glaciated territory as far north as Newfoundland; *Mexiterpes* has two species in Mexican caves that are disjunct from the remainder of the family by more than 1000 miles.

These speculations are summarized in Maps 1–4 and Diagram 1. No time scale is to be inferred in reading Diagram 1.

KEY TO GENERA OF THE CLEIDOGONIDAE, BASED ON MALES

1a. Dorsum with longitudinal rugae or several irregular series of small knobs; thick segmental shoulders usually well developed (Fig. 6), sides of segments longitudinally striate; anterior gonopod colpocoxites with a lateral branch bearing a gland channel (Figs. 1, 2). .... *Pseudotremia*

1b. Dorsum smooth; segments usually cylindrical, or with shoulders weakly developed, in a few species nearly horizontal paranota present (Fig. 274); anterior gonopod colpocoxites with gland channel obscure or absent 2

2a. Anterior gonopod colpocoxites with two large, subequal branches (Fig. 174), the anteriormost ornate and bearing a vague gland channel; Chiapas; Guatemala .... *Solaenogona*

2b. Anterior gonopod colpocoxites not as described above; usually with a single major branch (Figs. 184, 185) 3

3a. Anterior gonopod sterna with a pair of large projections (Fig. 416); most body segments with moderate paranota; Panama .... *Dybasia*

3b. Anterior gonopod sterna without processes, solidly joined to gonopod coxae (Figs. 184, 185) 4

4a. Posterior gonopod coxae elaborately lobed (Fig. 407), interlocking with simplified anterior gonopods; posterior gonopod sternum with a large knob (Fig. 402) .... *Tiganogona*

4b. Posterior gonopod coxae elongate, lobed (Fig. 199), but not to the extent as described above, not interlocking with anterior gonopods, which may be complex; posterior gonopod sternum without a knob (Fig. 199) .... *Cleidogona*

Genus *Pseudotremia* Cope

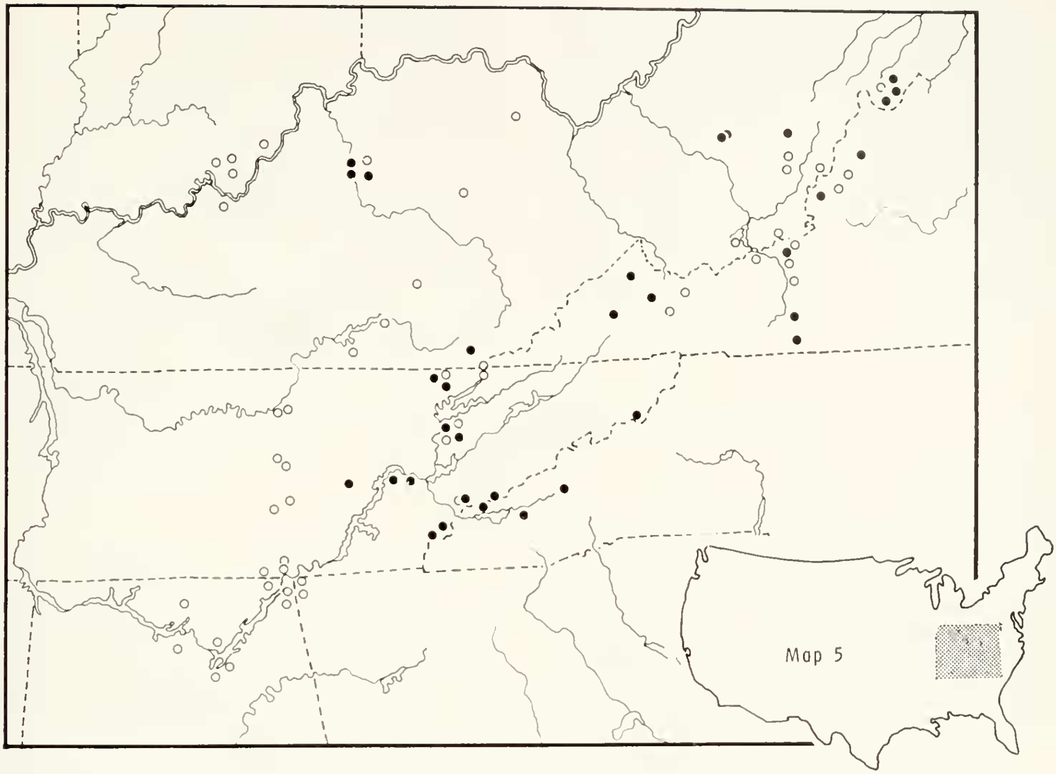
Pseudotremia Cope, 1869, Proc. Amer. Philos. Soc., 11: 179; Cook and Collins, 1895, Ann. New York Acad. Sci., 9: 34; Hoffman, 1950, J. Washington Acad. Sci., 40: 90; 1958, Proc. Biol. Soc. Washington, 71: 113–115; Chamberlin and Hoffman, 1958, Bull. U. S. Natl. Mus., 212: 94 (list of species).

Dearolfia Loomis, 1938, Bull. Mus. Comp. Zool., 86: 177.

Type species of *Pseudotremia, P. cavernarum* Cope, 1869, by monotypy; of *Dearolfia, D. lusciosa* Loomis, 1939, by monotypy. The meaning of the generic name *Pseudotremia* is apparently "false pore [*pseudo* + *trema* (pore, or hole)]" and may refer to Cope's mistaking the setal sockets for pores. The gender is feminine.

Diagnosis. The genus *Pseudotremia* is distinct from all but a few species of the Cleidogonidae in the tuberculate dorsum and the strong, rounded segmental shoulders on most species. The gonopods of the males bear a lateral branch on the colpocoxite, which carries a gland channel.

Description. Thirty segments. Mentum divided. Antennae long, article 3 or 5 the longest. Ocelli always present, though in many cases reduced in number (Figs. 36, 47), irregular in shape, and lacking pigment. Body fusiform, widest in males at segment 7, tapering evenly posteriad. Segments with more or less prominent rounded shoulders (Fig. 6), sometimes raised above the level of the dorsum, usually most prominent on segments 7–15, divided by a diagonal depression. Surface of segments rarely smooth, variously rugose, knobbed or striate. Sides of segments with 5–15 lateral striations. Segmental setae not prominent, short and spatulate in troglobitic species, becoming prominent posteriorly in most other species. Pregonopodal legs of males: legs 1 and 2 6-segmented, reduced slightly in size, genital openings on coxae of second legs on slightly raised knobs. Legs 3 through 7 strongly crassate, prefemora and femora enlarged and slightly curved mesad, tarsi with special setae very prominent. Coxae of leg 7 especially enlarged, often with prominent posterior knobs. Anterior gonopods: highly modified (Figs. 1, 2). Sternum partially fused to coxae, extending between colpocoxites as weakly sclerotized membrane; deeply depressed laterally at spiracle. Coxae not fused in midline, cupped and setose laterally. Colpocoxites with two main branches; lateral branch thin, evenly curved, often divided, bearing gland channel; median branch thick anteriorly, bladelike posteriorly, posterior edge laciniate, sometimes with subapical spine. Telopodites fused at base to each other and to coxae, various median processes arising from base of telopodites and projecting between colpocoxites; telopodites usually mitten-shaped,



Map 5. Appalachian region, showing distribution of species of the genus *Pseudotremia*. Dots, epigean records; circles, cave records. Only selected records for some species shown; some unidentifiable female and juvenile records also shown to give complete picture of distribution of genus.

curving anterioventrad. Posterior gonopods (Fig. 11): sternum bandlike, weakly sclerotized. Coxae enlarged, variously lobed; telopodites reduced, 4- to 2-segmented, claw always present. Tenth and eleventh legs with coxal glands. Tenth legs with more or less prominent knobs on coxal faces; eleventh legs with coxal knobs or hooks. Twelfth legs and sternum unmodified. Female cyphopods (Figs. 5, 16, 22) with valves flattened distally, fused proximally, often drawn out into processes and knobs, heavily setose. Postgenital plate always absent.

Distribution (See Map 5). Appalachian Mts. and interior foothills, frequently in caves, from southern Indiana through Tennessee to northeastern Alabama and northwestern Georgia, north through extreme western North Carolina to western Virginia and Pendleton Co., West Virginia, west to central Kentucky. Reported once (Williams and Hefner, 1928) from Adams Co., Ohio.

Gonopod Anatomy of *Pseudotremia*

The gonopods of *Pseudotremia hobbsi* are typical of those found in other members of the genus *Pseudotremia*. The description below was prepared from material cleared in trypsin.

In anterior view (Fig. 1), a continuous sternal bar (*S*), strongly sclerotized, extends between the origins of the tracheal apodemes (*TA*). The gonopod coxae (*C*) are not fused to each other, nor are they in contact mesally; they articulate with the sternum by means of a clasplike mechanism (*A*, Fig. 4) into which a projection

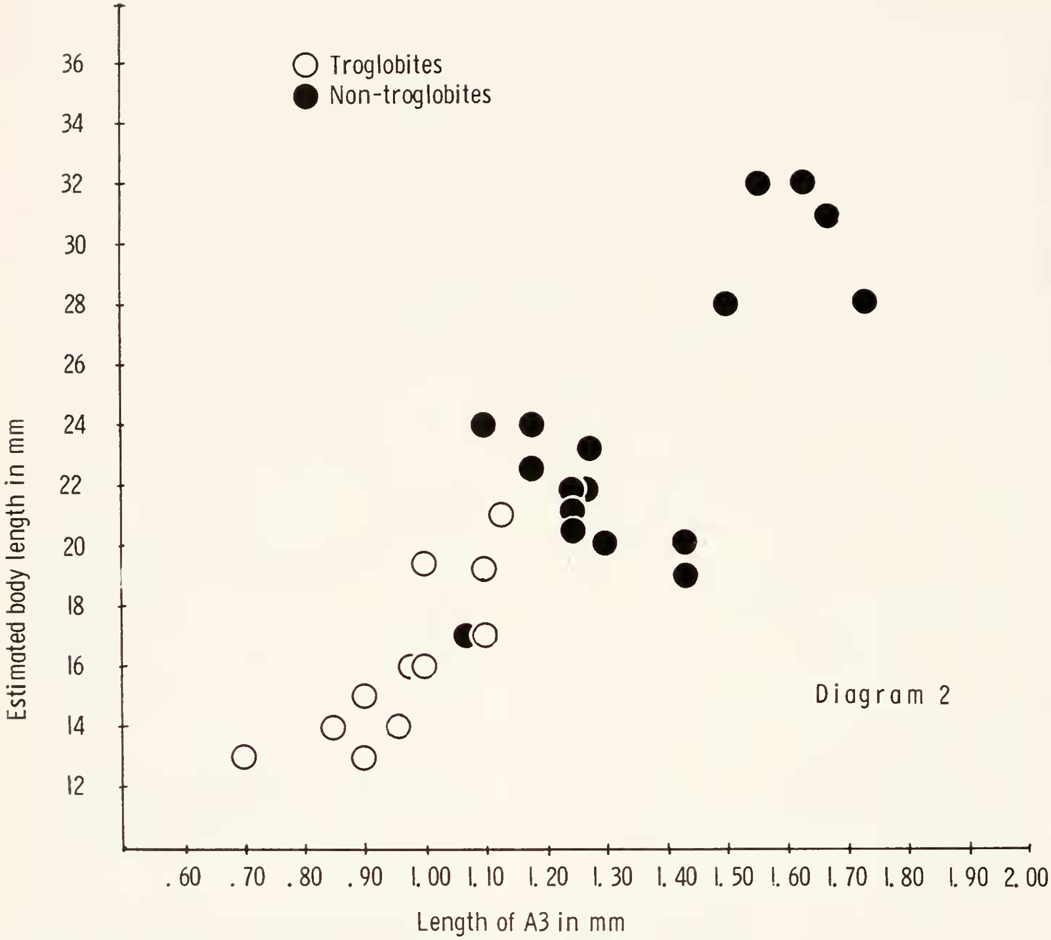


Diagram 2. Graph showing relationship between estimated body length and length of antennal segment three (A3) in holotypes of selected species of *Pseudotremia.*

from the sternum (*B*) inserts. Near the origin of the colpocoxites (*CC*) is an anteriorly projecting coxal knob (*CK*), which, as in *Cleidogona,* receives strong muscles from the tracheal apodeme of the opposite side. The colpocoxites (*CC*) are composed of a bladelike, curved lateral branch (*LB*) that in most species is forked, or bears a ventral tooth (*VB*). A gland channel (*G*) follows the dorsal part of the lateral branch. The mesal branch (*MB*) is thickened along the anterior margin, but tapers posteriorly to a thin, laciniate edge. Most species bear a subapical spine (*SA*), which in *hobbsi* is unusually long, and extends straight ventrad. The origin of the intergonopodal sclerite (*IGS*) is obscure. In uncleared preparations, it is more or less solidly fused to the bases of the telopodites. In *P. hobbsi,* as in many other species, it bears a process that is of considerable taxonomic value. The telopodites (*T*) are fused basally and bear a large knob. In all known species but one, they are similarly mitten-shaped, though their size varies considerably. In posterior view (Fig. 2), little more is revealed. Here it can be seen that the sternum is incomplete posteriorly, as in *Cleidogona,* but a lateral sternal sclerite is not definitely set off. Finally, in a slightly dorsal view of the base of a gonopod coxa (Fig. 3), the gland channel (*GC*) can be seen to begin in a definite internal pore (*P*).

There is surprisingly little variation in overall plan in the gonopods of species of *Pseudotremia.* In extreme troglobites (*P. cercops,* Fig. 81; *P. nodosa,* Fig. 70), everything is much simplified. In *P. sublevis* (Fig. 168), the ventral part of the lateral branch of the colpocoxite is very large, and the mesal branch reduced in size. In *P. stupefactor,* (Fig. 27), the telopodites are enormously enlarged and cover the remainder of the gonopods.

Cyphopod Anatomy of *Pseudotremia*

The cyphopods of female millipeds are cuticular specializations surrounding the pores of the oviducts, and are located posterior to the coxae of the second legs (Fig. 7). In *Pseudotremia hobbsi,* most features of taxonomic importance, especially the general shape of the organs, are visible without special treatment. After clearing in trypsin, however, several interesting structures come to light. The coxae (*C*) and sternum (*S*) of the second legs (Fig. 5) surround the cyphopods anteriorly. The coxae of the third legs are not strongly modified, but only shallowly excavate on their anterior faces. Each cyphopod is composed of four main parts. The valves are posteriormost and are fused dorsally, though in some cases (*P. lethe,* (Fig. 7) the fusion is nearly complete ventrally as well. The mesal valve (*MV*) is usually the longest, the lateral valve (*LV*) the broadest. In the groove between the valves, the sinuous seminal receptacle can be seen. Anteriorly, the unfused portions of the valves are capped by the receptacle (*R*), which in *P. hobbsi* bears a series of processes that may lock the subapical spine of the gonopod in place during copulation. Posterior to the receptacle and surrounding the actual oviduct pore (*O*) are two pairs of sclerotized bars that cannot be seen in uncleared material. These post-receptacular bars (*PB*) were noticed by Buckett and Gardner (1967) in *Idagona westcotti,* but are not shown in any of the many European chordeumids illustrated by Bröleman (1935). In reality, the valves and receptacle of *Pseudotremia* cyphopods are heavily setose. These setae have been omitted for clarity in the drawings presented here, and in those that follow in the taxonomic part.

Species Characters and Evolution of Gonopods in *Pseudotremia*

It is difficult at this time to make any definite statements about the possible course of gonopod evolution in the genus *Pseudotremia.* Little is known of the functional significance of various features, and many species remain to be discovered and described. The present total of 36 species presents a complex array of gonopod types, some few of which (*P. stupefactor,* Fig. 28; *P. sublevis,* Fig. 169) seem quite unrelated to the others.

However, a few general statements can be made. The size of the gonopods is usually in keeping with the size of the animals —no small species have greatly enlarged gonopods and no large ones have unusually small gonopods. In general, the most complex kinds of gonopods are found in the largest (and usually) epigean species; the smallest and simplest gonopods are to be found in the smallest and most highly specialized troglobites.

Some features of the gonopods seem more subject to variation than others. In *P. hobbsi,* three distinct forms of lateral branch of the colpocoxite are found in three different localities, but the variation is only in the relative sizes of the branches (Figs. 163–165). In most cases, the presence or absence of a division in the lateral branch of the colpocoxite is a good species character, but it is probably subject to varying selection pressures; in *P. carterensis* (Fig. 141) the ventral part is reduced

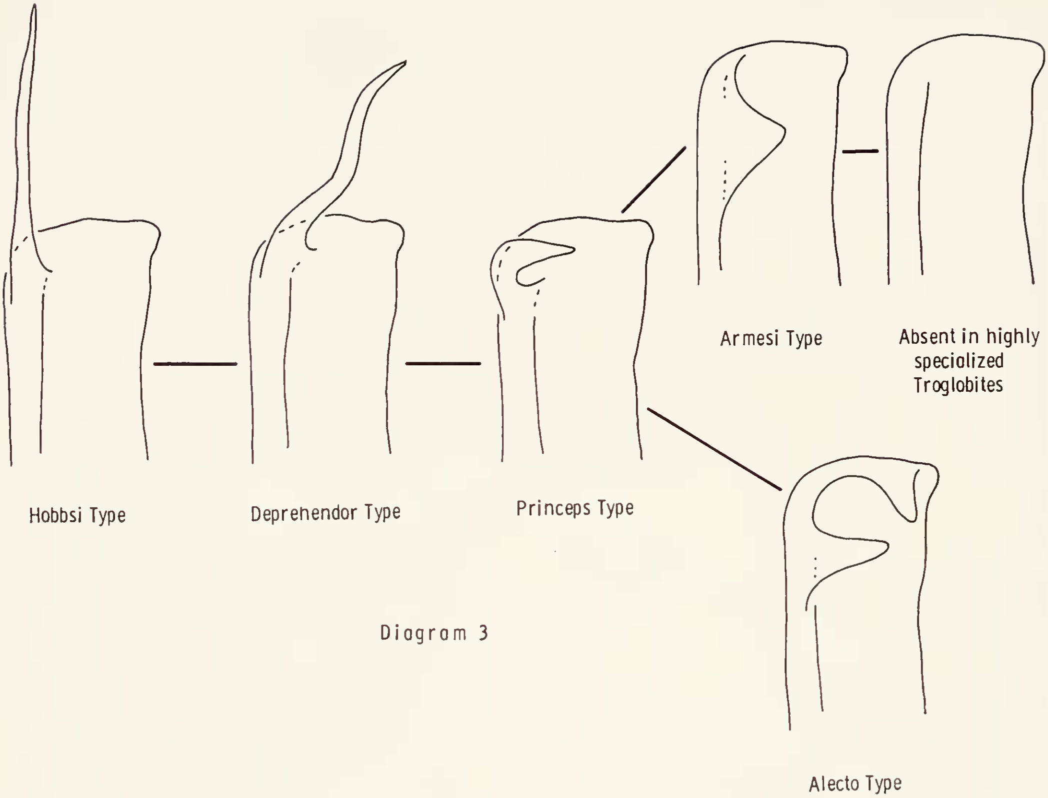


Diagram 3. Types of subapical spines on median colpocoxites of gonopods of *Pseudotremia* species. Heavy lines indicate hypothetical relationships but do not imply direction of evolution.

to a small tooth. There seems to be a tendency for branching to be suppressed. In troglobites with simplified gonopods (*e. g., P. lictor,* Fig. 86) the lateral branch of the colpocoxite is always simple. However, *P. sublevis* (Fig. 168) has the ventral branch of the lateral colpocoxite enormously enlarged.

The relative size of the telopodites in comparison with the colpocoxites is also variable, with a tendency for larger telopodites to occur in species in which the colpocoxites are less complex. *Pseudotremia stupefactor* (Figs. 27, 28) has the telopodites greatly expanded and curving over to cover the colpocoxites. I cannot even guess at the functional significance of this modification; the telopodites are not movable. But in general, the telopodites do not provide many good taxonomic characters.

The subapical spine of the mesal colpocoxite is absent in troglobites with simplified gonopods, but is also absent in many epigean species with otherwise complicated gonopods. A number of types can be discerned in species where this spine is present. In *P. hobbsi* (Figs. 1, 2) the spine is extremely long and may be a locking device that fits into prongs on the cyphopod receptacle during mating. This *hobbsi* type grades into a form that is likewise long, but curved, that may be termed the *deprehendor* type (*P. deprehendor,* Fig. 145). Most common is the *princeps* type, in which the spine is short and very distinctly bent mesad (*P. princeps,* Fig. 148); the *armesi* type, in

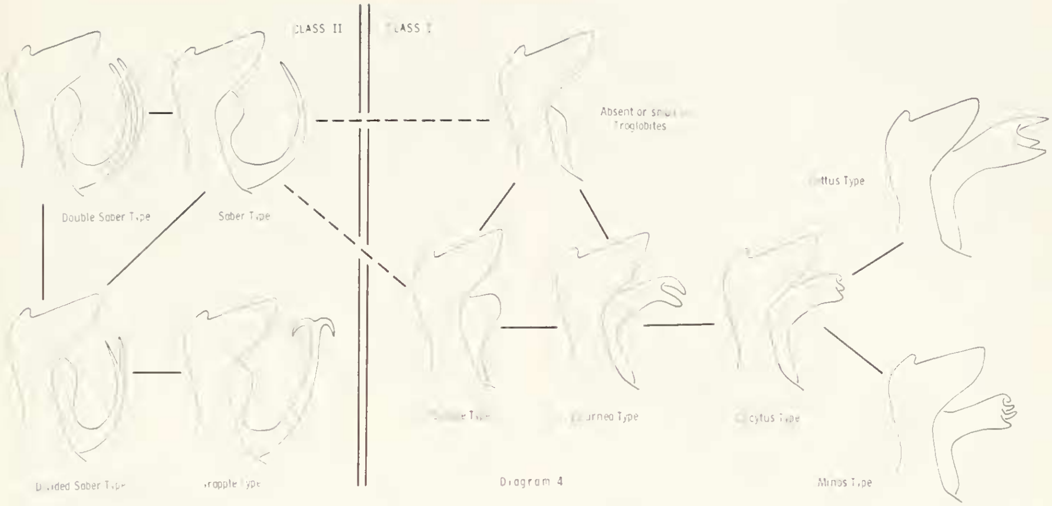


Diagram 4. Classes and types of telopodite processes of gonopods of *Pseudotremia* species. Heavy lines indicate hypothetical relationships, dashed lines more speculative ones; neither kind of line implies direction of evolution. Double line is artificial division between Classes I and II.

which the spine occurs only as a triangular lamella (*P. armesi*, Fig. 118), and the *alecto* type (*P. alecto*, Figs. 122, 123), in which a distinct excavation above the spine gives the impression of a forcepslike apparatus, may be only subtypes of the *princeps* group. It is once again difficult to suggest in which direction this character is evolving, towards loss of the spine or towards its hypertrophy, but some possible relationships are summarized in Diagram 3. The absence of this spine, or its form when present, are good species characters.

The telopodite process is an extremely important taxonomic character, since it is rarely alike in two species. Once again, the process is absent in extreme troglobites. There is some individual variation in species that are widespread enough to slow down or limit gene flow between populations; two forms (Figs. 103, 104) occur in *P. cottus*. Telopodite processes are divisible into two large categories. In the first class, the process arises from the bases of the telopodites and projects straight anteriad from the notch between them (*Class I*, Diag. 4). In the second, the process begins near the notch as a more or less well-developed knob, but then curves dorsad between the coxae (*Class II*, Diag. 4).

Five smaller groups can be recognized within the first class. The simple type consists of a short undivided knob or a broadly flattened lamella (*P. spira*, Fig. 44). In the *eburnea* type, the knob is divided at the apex (*P. rhadamanthus*, Fig. 54). In two types, the apical part of the process is divided into three branches; these branches are blunt in the *cocytus* type (*P. cocytus*, Fig. 99), and much larger and pointed in the *cottus* type (*P. cottus*, Fig. 103). The *minos* type occurs only in *P. minos* (Fig. 95) and seems to be a development from one of the two preceding kinds. Diagram 4 summarizes the forms of these processes and presents some ideas on their possible relationships. Geographically, with the exception of the two three-pronged kinds, the different ones seem at present to be distributed at random.

Under the second class, four basic types are clearly separable. In the saber type, the process is single and uniformly curved (*P. fulgida*, Fig. 135). The *divided* saber type (*P. merops,* Fig. 31) is split at the tip, and the double saber type is completely divided (*P. deprehendor,* Fig. 145). The relationships of the grapple type are obscure (*P. indianae,* Fig. 18), but it probably represents a specialization of the divided saber type. The groups are not coherent geographically, but there is a tendency for the various types of Class II to occur in the northern part of the range of *Pseudotremia.* Diagram 4 represents a summary of the above information.

The trend in the evolution of the posterior gonopods is obvious; they are becoming progressively reduced in size and number of segments. In the simplest forms (*P. lictor,* Fig. 87), only two segments are movable with respect to each other; the apical three segments do not have joints between them. However, the claw is present in all species. The form of the posterior gonopods can be useful in separating species, but breaks down when species are closely related.

No particular evolutionary changes can be discerned at this time in the cyphopods. Because of their greater simplicity and variability (see Figs. 21–23, 106–109, 138–140), they are of less use than the gonopods in taxonomy. Females are not known for many previously described species, and thus I have not attempted to give names to females not associated with males.

Finally, an unusual feature of *Pseudotremia* among chordeumids is the usefulness of some nonsexual characters in separating species. The degree and pattern of dorsal tuberculation ranges from only a few low rugae to 40 or more well-defined nodules on each segment. The relative size of the segmental shoulders is also a good character; some species are more like *Cleidogona,* with low swellings, while others have the dorsum nearly flat, owing to the high shoulders. The shoulders generally become less prominent on posterior segments, and the point at which they are reduced to the level of the lateral striae is of taxonomic value. The number and distinctness of the lateral striae is of lesser importance.

Body length is of limited value, and difficult to measure consistently, owing to telescoping and/or coiling of the body. The lengths given for each species below are thus approximate. The length of the third antennal segment (A3) is correlated with body length (Diag. 2), and thus is given for the types of each species. Troglobitic species (open symbols, Diag. 2) do not appear to have this segment longer in relation to body length than do epigean ones.

KEY TO MALES OF *PSEUDOTREMIA* SPECIES

1a. Telopodites greatly enlarged, arching over and covering colpocoxites, nearly touching sternum in front (Figs. 27, 28); north-central Kentucky ..... *stupefactor*
1b. Telopodites usually smaller than or subequal to colpocoxites 2
2a. Lateral branch of colpocoxite divided 3
2b. Lateral branch of colpocoxite not divided 21
3a. Subapical spine of median colpocoxite absent 4
3b. Subapical spine of median colpocoxite present, or a small triangular lamella present on mesal subapical edge of median branch 9
4a. Telopodite process absent or almost so; troglobitic; Jackson Co., Tenn. ..... *lethe*
4b. Telopodite process present, of various forms 5
5a. Telopodite process grapplelike; ventral branch of lateral colpocoxite very long (Fig. 110); Tazewell Co., Va. ..... *tuberculata*
5b. Telopodite process not as above 6
6a. Telopodite process small, saberlike; ventral branch of lateral colpocoxite large, broad, L-shaped (Fig. 168); median colpocoxite reduced; Giles Co., Va. ..... *sublevis*
6b. Telopodite process not as above 7
7a. Telopodite process blunt, apically cleft (Fig. 50); troglobitic; Van Buren and Warren Cos., Tenn. ..... *acheron*
7b. Telopodite process divided into three short branches (Figs. 99, 103, 104); not troglobitic; large pigmented species 8
8a. Telopodite process relatively small (Fig. 99), branches blunt; Anderson Co., Tenn. ..... *cocytus*
8b. Telopodite process very large (Fig. 104); branches pointed; several counties in east Tennessee (Map 7) ..... *cottus*

9a. Telopodite process absent or a small knob 10
9b. Telopodite process present, or other than a knob 11
10a. Telopodite process absent; lateral branch of colpocoxite narrow (Fig. 59); about 14 ocelli; western North Carolina .... *soco*
10b. Telopodite process a small knob, lateral branch of colpocoxite broad (Fig. 148); about 20 ocelli; Pendleton Co., W. Va. .... *princeps*
11a. Telopodite process of the saberlike type, split at the tip (Fig. 9), single (Fig. 135) or double (Fig. 145), or grapplelike (Fig. 18) 12
11b. Telopodite process not of the saberlike form, blunt (Figs. 63, 89) 20
12a. Telopodite process grapplelike (Fig. 18) 13
12b. Telopodite process otherwise 15
13a. Median colpocoxites strongly decurved (Fig. 115); Smyth and Bland Cos., Va. .... *momus*
13b. Median colpocoxite erect 14
14a. Dorsum with numerous small, well-defined tubercles; 13–17 ocelli; usually not pigmented; caves in southern Indiana .... *indianae*
14b. Dorsum with several strong rugae; 19–21 ocelli; pigmented; Mercer Co., W. Va. .... *armesi*
15a. Telopodite process saberlike, apically divided 16
15b. Telopodite process saberlike, not divided 17
16a. About 12 ocelli; Clark Co., Ind. .... *nefanda*
16b. About 19–20 ocelli; Alleghany Co., Va. .... *alecto*
17a. Not pigmented; dorsum heavily knobbed; about 14 ocelli; Meade Co., Ky. .... *amphiorax*
17b. Pigmented; dorsum nearly smooth; ocelli usually more than 15 18
18a. 20–24 ocelli; body 30 mm long or longer 19
18b. 15–17 ocelli; body length rarely more than 25 mm .... *cavernarum*
19a. Smaller branch of lateral colpocoxite recurved (Fig. 152); Pocahontas Co., W. Va. .... *tsuga*
19b. Smaller branch of lateral colpocoxite not recurved (Figs. 163–165); eastern West Virginia and adjacent Virginia (Map 8) .... *hobbsi*
20a. Telopodite process with two blunt lobes (Figs. 63, 64); about 12 ocelli; tuberculation of dorsum weak; Dade Co., Ga. .... *eburnea*
20b. Telopodite process with three blunt lobes (Fig. 90); 25–30 ocelli; dorsum of each segment with 30–40 prominent tubercles; Scott Co., Tenn. .... *scrutorum*
21a. Subapical spine of median branch of colpocoxite absent 22
21b. Subapical spine of median branch of colpocoxite present, or a small triangular lamella present on mesal subapical margin of median branch 27
22a. Telopodite process a large, saberlike spine, single (Fig. 135) or double (Fig. 31), extending between coxae 23
22b. Telopodite process a blunt knob, or absent 24
23a. Telopodite process single (Fig. 135); body nearly smooth dorsally; 5–7 ocelli; Greenbriar Co., W. Va. .... *fulgida*
23b. Telopodite process double (Fig. 31); body with 30–40 strong dorsal knobs per segment; about 12 ocelli; Adair Co., Ky. .... *merops*
24a. Telopodite process knoblike; median colpocoxites sharply turned outward, lateral colpocoxites spiral in anterior view (Fig. 44); Pulaski Co., Ky. .... *spira*
24b. Telopodite process absent; colpocoxites short, simple 25
25a. About 12 ocelli; segmental shoulders very high, 4–5 strong knobs per segment on dorsum (Fig. 6); Marshall Co., Alabama .... *nyx*
25b. Less than 8 ocelli; segmental shoulders low 26
26a. Gonopods as in Fig. 81; dorsal tubercles inconspicuous; DeKalb Co., Tenn. .... *cercops*
26b. Gonopods as in Fig. 85; 12–15 large tubercles per segment; DeKalb Co., Tenn. .... *lictor*
27a. Subapical spine of median colpocoxite in the form of a triangular lamella (Fig. 66) 28
27b. Subapical spine of median colpocoxite in the form of an acuminate spine (Fig. 128) 29
28a. About 16 ocelli; segmental shoulders of moderate size; Dade Co., Georgia .... *aeacus*
28b. Eight to 11 ocelli; segmental shoulders low; Claiborne Co., Tenn. .... *nodosa*
29a. Telopodite process absent 30
29b. Telopodite process of various forms 32
30a. Adult males less than 25 mm long 31
30b. Adult males 30 mm long or more .... *simulans*
31a. Pigmented animals, 20–22 ocelli; Claiborne Co., Tenn. .... *valga*
31b. Colorless animals, 7–9 ocelli; Rockcastle Co., Kentucky .... *unca*
32a. Telopodite process saberlike, single (Fig. 141) or double (Fig. 145) 33
32b. Telopodite process a knob with 4 short spines (Fig. 95); Jackson Co., Ala. .... *minos*

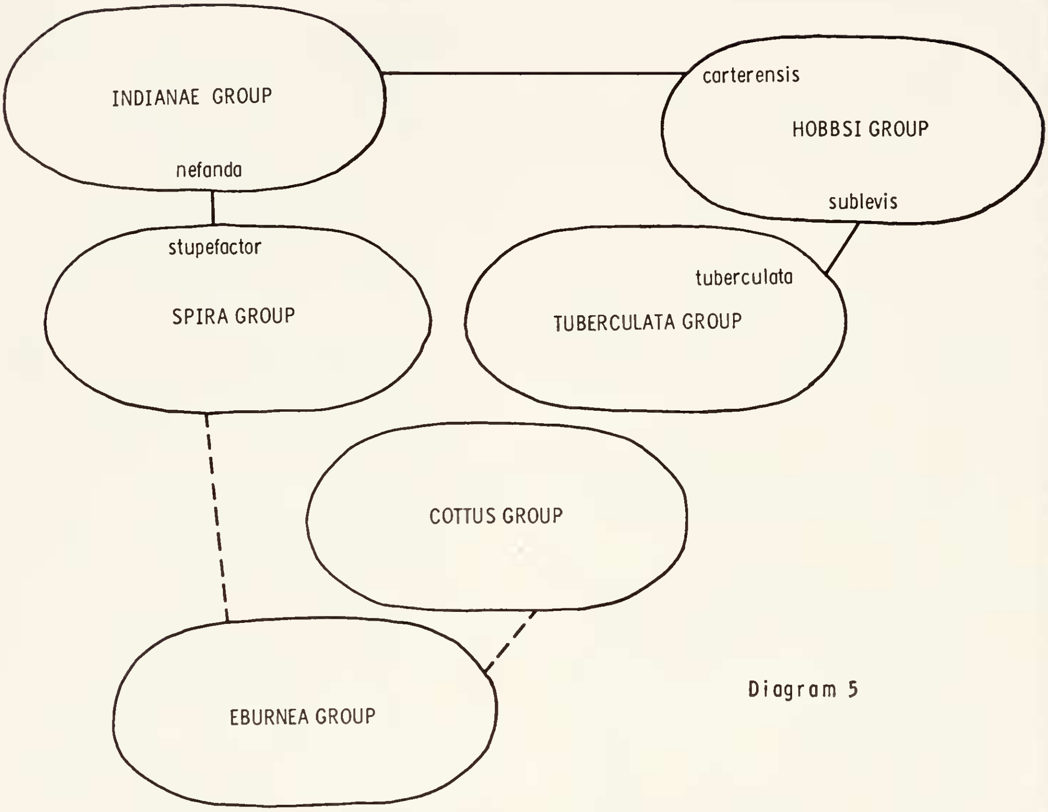


Diagram 5. Possible relationships between species groups of *Pseudotremia*. Species that give good evidence for this arrangement are named close to lines connecting groups; lines do not imply direction of evolution. Species groups arranged in this diagram roughly as they are distributed geographically; compare Map 5.

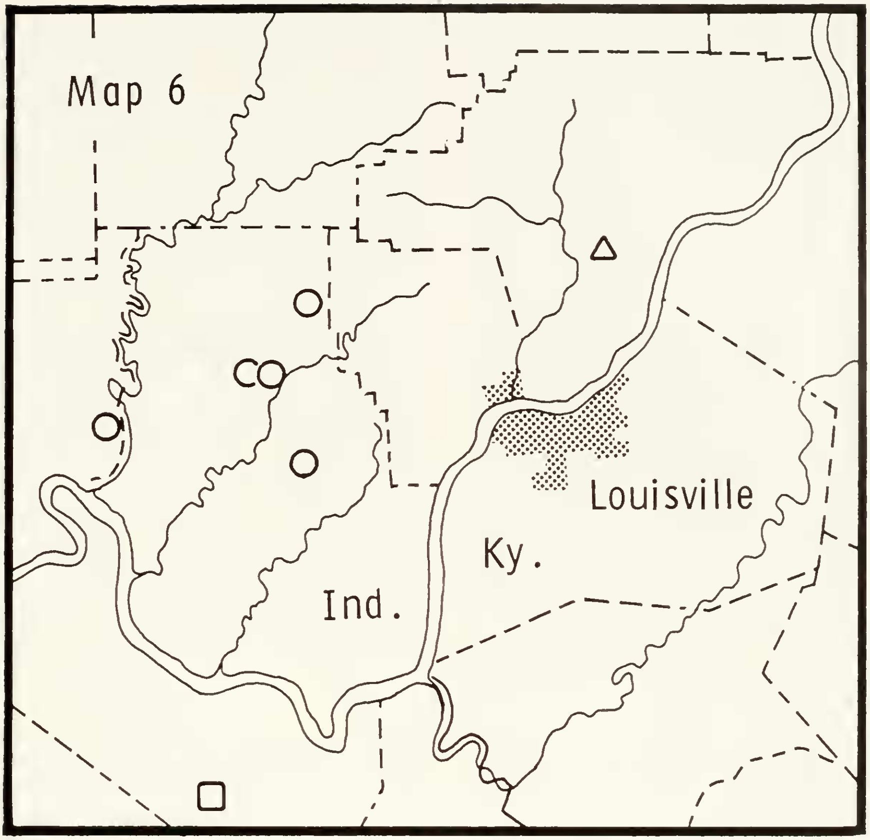
33a. Telopodite process of the double saber type (Fig. 145); Anderson Co., Tenn. ... *deprehendor*
33b. Telopodite process a single saber ... 34
34a. Eighteen to 20 ocelli; gonopods as in Fig. 141; Carter Co., Ky. ... *carterensis*
34b. Five to 8 ocelli; gonopods as in Figs. 125, 126; Pendleton Co., W. Va. ... *lusciosa*

Species Groups in *Pseudotremia*

The arrangement of the species discussed here is admittedly a somewhat artificial one. As I have already mentioned, there are many species as yet undiscovered and undescribed; perhaps they will later fill gaps that will make possible more natural groupings. The species groups I propose are based on a combination of morphological evidence (mostly drawn from male gonopods) and geographical distribution. *Pseudotremia carterensis* and *P. deprehendor,* for example, are placed in the *hobbsi*-group, but are widely separated from the other species of the group geographically.

The arrangement of species into groups that are more or less coherent geographically and perhaps phylogenetically related makes it possible to compare each species only with those closest to it in the species diagnoses given below.

The relationships between groups expressed in Diagram 5 is likewise speculative, and is based on evidence presented in the species descriptions below.



Map 6. Parts of Indiana and Kentucky, showing distribution of species of the genus *Pseudotremia*. Circles, *P. indianae*; triangle, *P. nefanda* type locality; square, *P. amphiorax* type locality.

THE *INDIANAE* GROUP

The three species of this group occur in southern Indiana and adjacent Kentucky (Map 6). All have divided lateral colpocoxites and a spine on the median colpocoxite. The form of the telopodite process is variable. All lack pigment to some degree, with the ocelli reduced in number; they are known only from caves.

Pseudotremia nefanda n. sp.
Figures 8–12, Map 6

Types. Male holotype, female paratype and several other specimens of both sexes from Indian Cave, 0.7 mi. west of Charleston, Clark Co., Indiana, collected 26 January 1957, by T. C. Barr. The specific name is an adjective, meaning "confusing."

Diagnosis. Distinct from all other members of the *indianae*-group in the apically divided saberlike telopodite process, and in having slight pigmentation. The dorsum is not as knobby as in *P. amphiorax*, but slightly more so than in *P. indianae*.

Description of male holotype. Length, 15 mm, A3 = 1.08 mm. Ocelli irregular in shape and arrangement, 16 on either side, only partly pigmented. Coloration pale brown, vaguely marked darker purplish brown anteriorly. Segmental shoulders low, reduced to level of lateral striae about segment 15; dorsum moderately strongly tuberculate, rugae and knobs well defined on posterior segments. Lateral striae prominent, 10–12 on midbody segments. Anterior gonopods: median colpocoxite with subapical spine (Figs. 8, 9), secondary spine projecting laterad from base of subapical spine; lateral colpocoxite short, simply curved, apically divided (Fig. 10), gland channel becoming obscure before division. Telopodite process short, curved dorsad, then slightly ventrad, apically cleft (Fig. 8). Telopodites as usual for the genus, but quite large, curving strongly anteriad. Posterior gonopods: coxa deeply excavate (Fig. 11), second article as long as coxa, 3 distal articles as usual, not conspicuously reduced.

Description of female paratype. Length, 14 mm, A3 = 1.06 mm. Other nonsexual characters as described for male. Cyphopods (Fig. 12): mesal valve narrow, elongate, lateral valve anteriorly lobed, wide; valves well separated.

Distribution. Known only from the type locality.

Pseudotremia amphiorax n. sp.

Figures 13–16, Map 6

Types. Male holotype, female paratype and several other specimens of both sexes from Sig Shacklett's Cave, 3 mi. north of Big Spring, 1.25 mi. north of Maples Corner, Meade Co., Indiana, collected 13 July 1957 by T. C. Barr. The specific name is a noun in apposition, the name of an argonaut and soothsayer.

Diagnosis. Distinct from the other species of the *indianae*-group in the short, undivided saberlike form of the telopodite process and the extremely rough dorsum. The posterior gonopods are also much smaller than in the other species.

Description of male holotype. Length, 15 mm, A3 = 0.90 mm. Ocelli irregular in shape and distribution, not pigmented, 14 on left side, 15 on right side. Body lacking pigment. Segmental shoulders moderately high, reduced to level of lateral striae by segments 12–14; dorsum extremely rough, especially on posterior segments, about 30 prominent discrete tubercles on each midbody segment. Lateral striae strong, 9–10. Anterior gonopods: median colpocoxite with sharply recurved subapical spine (Fig. 15) broad at base, not branching from median colpocoxite until about one-half length of median colpocoxite, branches diverging at nearly right angles, ventral branch curved ventrad, then mesad, gland channel following shorter dorsal branch. Telopodite process short, curved, acuminate. Telopodites (Fig. 14) large, fused for most of their length, slightly curved anteriad. Posterior gonopods (Fig. 15): small, coxae deeply excavate mesally and lobed, second article somewhat longer than coxae, 3 apical articles greatly reduced.

Description of female paratype. Length, 15 mm, A3 = 0.93 mm. Nonsexual characters as in male. Cyphopods (Fig. 16) with lateral valve small, unmodified; median valve with distal processes.

Distribution. Known only from the type locality.

Pseudotremia indianae Chamberlin and Hoffman

Figures 17–24, Map 6

Pseudotremia cavernarum, Cook and Collins, 1895, Ann. New York Acad. Sci., 9: 36–39, figs. 2–7, ♂. Not *P. cavernarum* Cope.

Pseudotremia indianae Chamberlin and Hoffman, 1958, Bull. U. S. Nat. Mus., 212: 95. New name for Cook and Collins' specimens of *P. cavernarum.*

Types. According to Chamberlin and Hoffman (1958) the types of *P. indianae* are in the U. S. National Museum. They could not be located. The specimens described below were compared to a series of badly preserved specimens in the MCZ, collected at the type locality (Wyandotte Cave, Crawford Co., Indiana) by E. D. Cope in 1885, and found to be conspecific with them.

Description of male from King's Cave. Length, 17 mm, A3 = 1.05 mm. Ocelli 15 on both sides, irregularly arranged, not pigmented. Body not pigmented. Segmental shoulders strong, reduced to level of lateral striae on segments 20–22; dorsum heavily tuberculate, about 25 low knobs per midbody segment; lateral striae 10–13. Anterior gonopods: median colpocoxite (Fig. 18) with subapical spine directed sharply dorsad and anteriad; lateral colpocoxite (Figs. 18, 19) divided, branches diverging at less than right angle, path of gland channel becoming obscure near branching point. Telopodite process (Figs. 17, 18) extremely large, curving in an arc of a circle between, then above, colpocoxites of each side, divided apically, divisions recurved, forming a grapplelike structure. Telopodites (Fig. 17) of moderate size. Posterior gonopods (Fig. 20) similar to those of *nefanda*.

Description of female from King's Cave. Length, 17.5 mm, A3 = 1.00 mm. Nonsexual characters as in male, but most females have slightly more (17–20) ocelli. Cyphopods (Fig. 21) similar to those of *nefanda*.

Distribution. Southern Indiana, in caves (Map 6). The following specimens were examined: INDIANA: *Crawford Co.*, Wyandotte Cave, E. D. Cope, 1885, ♂♂ ♀♀; *Harrison Co.*, Byrnes Cave, 1 mi. east of New Salisbury, T. C. Barr, 4 August 1957, ♂ ♂, juveniles; Steersetter Cave, 0.5 mi. east of Salisbury, T. C. Barr, 4 August 1957, ♂♂ ♀♀; Bevin Cave, 1 mi. north of Byrneville, T. C. Barr, 4 August 1957, ♂♂ ♀♀; King's Cave, 3.5 mi. east of Corydon, 17 August 1957, T. C. Barr, ♂♂ ♀♀; L. Hubricht, 12 August 1957, ♂♂ ♀♀.

Notes. The number of ocelli in males varies from 14–19, average 15; females have 17–20 ocelli, average 19. There is little discernible variation in the male gonopods from the localities listed above, but the female cyphopods are somewhat variable; compare Figures 21–23. The confusion of Cook and Collins (1895) as to the identity of *Pseudotremia* from Indiana caves was engendered by Cope and Packard, who labelled all troglobitic specimens of *Pseudotremia* as *cavernarum*. Cope's original collection of *cavernarum* from Erharts Cave, Montgomery County, Virginia, was not available to Cook and Collins, but Hoffman (1958) showed that the species found at the type locality of *cavernarum* is not the same as the species in Wyandotte Cave, Indiana, source of Cook and Collins' material. See further discussions under *P. cavernarum* and *P. carterensis*.

THE *SPIRA* GROUP

This group of troglobitic, troglophilic and epigean species occurs in both the Bluegrass and Cumberland Rim karst regions. Morphologically, the group is a heterogeneous one, including species with and without subapical spines on the median colpocoxites, and with divided and entire lateral colpocoxites. The telopodite process is either absent, present as a small knob, or as a divided saber. The affinities of the group are clearly with the *indianae*-group, and I think that when the list of species included is more complete, the groups may be combined. *Pseudotremia merops* has a divided saberlike telopodite process like that of *P. nefanda* of the *indianae*-group. The larger-than-normal telopodites of *nefanda* and *amphiorax* of the *indianae*-group may indicate affinities with the peculiar *P. stupefactor* of the *spira*-group.

Species of the *spira*-group resemble each other only in general gonopod morphology and geographic distribution; this group may prove to be the most unnatural of all.

Pseudotremia valga Loomis
Figures 24–26

Pseudotremia valga Loomis, 1943, Bull. Mus. Comp. Zool., 92: 377–378, figs. 2a–c, ♂.

Types. Male holotype from King Solomon's Cave, Cumberland Gap, Claiborne Co., Tennessee, collected 26 July 1924 by G. P. Englehardt, in MCZ, examined. King Solomon's Cave is not listed in *Caves of Tennessee* (Barr, 1961). *Caves of Virginia* (Douglas, 1964: 318) states that Cudjo's Cave, Cumberland Gap, Virginia, was at one time known as King Solomon's Cave. The town of Cumberland Gap is in Virginia. Thus I believe the type locality is probably Cudjo's Cave, Cumberland Gap, Lee Co., Virginia. The specific name is a Latin adjective, meaning "bow-legged."

Diagnosis. The median colpocoxites are widely separated at the base and curve sharply mesad; in all other species of the *spira*-group they are nearly parallel.

Description of male holotype. Length, 22 mm, A3 = 1.14 mm. Ocelli regular in size, pigmented, 20 on left side, 22 on right, in 6 rows forming triangular eye-patch. Coloration medium brown, marked darker purplish brown, especially on anterior segments. Segmental shoulders strong, reduced to level of lateral striae about segments 20–23; dorsum nearly smooth anteriorly, weakly rugose on midbody segments, posterior segments with posterior rows of 6–8 moderate tubercles; lateral striae prominent, 10–13. Anterior gonopods: median colpocoxite (Fig. 24) with strong subapical spine directed mesad; lateral colpocoxite (Fig. 25) broad, divided at apex, divisions subequal, curved mesad, meeting those of other side in midline. Telopodite process absent. Telopodites (Figs. 24, 25) broad, slightly curved. Posterior gonopods (Fig. 26) with second segment slightly longer than coxa, 3 apical segments as usual in larger species.

Distribution. Known only from the type locality, but undoubtedly occurs in other caves in the vicinity. The limestone stratum in which the type cave is located extends unbroken northward to the head of the Powell River valley and southwestward from there to near Sunbright, Va. (Douglas, 1964: 319).

Notes. Loomis (1943) had females available when the species was described, but their present whereabouts are unknown. In addition to the holotype, I examined a male collected at the type locality by T. C. Barr, 5 July 1958.

Pseudotremia stupefactor n. sp.

Figures 27–30

Types. Male holotype from cedar woods at Camp Nelson, Jessamine Co., Kentucky, collected 30 May 1958 by Leslie Hubricht; female paratype from Bowen Cave, 1 mi. northeast of Slade, Powell Co., Kentucky, collected with a male and other females 31 August 1957 by Leslie Hubricht. The specific name is a Latin noun in apposition, meaning "one who astonishes."

Diagnosis. Easily separated from any other known species of *Pseudotremia* by the enormous telopodites of the gonopods, which curve anteriad to cover the colpocoxites. Females have the median valve of the cyphopods very long.

Description of male holotype. Length, 21 mm, A3 = 1.17 mm. Twenty ocelli on both sides of head in 5 regular rows forming triangular ocellarium. Body gray-brown, weakly marked darker brown. Segmental shoulders moderate, reduced to level of lateral striae on segments 26; dorsum nearly smooth, with few weak rugae; lateral striae moderate, 9–14. Anterior gonopods: median colpocoxite with subapical spine directed anteriad (Fig. 27); lateral colpocoxite simple, evenly curved, not divided (Fig. 28). Telopodite process (Fig. 28) a small knob. Telopodites (Figs. 27, 28) enormously enlarged, curved sharply anteriad at an acute angle, covering colpocoxites, slightly recurved at tips, apparently not movable. Posterior gonopods (Fig. 29) typical, but coxae rather slender.

Description of female paratype. Length 22 mm, A3 = 1.19 mm. Nonsexual characters as in male. Cyphopods (Fig. 30) with median valve greatly elongated, almost acuminate posteriorly.

Distribution. In addition to the type and paratype localities, I examined the following specimens: KENTUCKY: *Anderson Co.*, Kentucky R. bluffs north of Tyrone, collector and date not given, ♀♀; *Mercer Co.*, Kentucky R. bluffs north and east of Shakertown, collector and date not given, ♀.

Pseudotremia merops n. sp.
Figures 31–35

Types. Male holotype and female paratype from Saltpetre Cave, 1 mi. northeast of Breeding, Adair Co., Kentucky, collected 3 August 1957 by L. Hubricht. The specific name is a noun in apposition, the name of a famous seer and soothsayer.

Diagnosis. No other *Pseudotremia* species has a divided saber-type telopodite process and colpocoxites without modification (Figs. 31, 32).

Description of male holotype. Length, 24 mm, A3 = 1.26 mm. Ocelli 12 on either side of head, irregularly arranged, weakly pigmented. Coloration typical purplish gray-brown, marked darker. Segmental shoulders large and prominent, reduced to level of lateral striae about segment 20; dorsum strongly knobbed, about 30 well-defined tubercles per segment; lateral striae vague, about 12 per segment on each side. Anterior gonopods: median colpocoxite (Fig. 31) large, upright, without subapical spine; lateral colpocoxite much shorter (Figs. 31, 32), evenly curved, entire. Telopodite process (Figs. 31, 33) short, curved ventrad, divided saber type. Telopodites (Fig. 31) widely diverging, smaller than colpocoxites. Posterior gonopods (Fig. 35) as usual.

Description of female paratype. Length, 25 mm, A3 = 1.25 mm. Nonsexual characters as in male. Cyphopods (Fig. 34) with lateral valve the largest, broadened and ventrally flattened.

Distribution. Known only from type locality.

Pseudotremia unca n. sp.
Figures 36–43

Types. Male holotype, female paratype and a second female from Great Saltpetre Cave, 4.6 mi. north of Livingston, Rockcastle Co., Kentucky, collected 15 December 1956 by T. C. Barr. The specific name is a Latin adjective, meaning "elbowed."

Diagnosis. Differs from *P. valga* in having undivided lateral colpocoxites; from the other species of the group in the sharp distal bend in the median colpocoxites and the small telopodites.

Description of male holotype. Length, 14 mm, A3 = 0.85 mm. Ocelli 7 on left side, 8 on right side (Fig. 36), irregular in shape and arrangement, without pigment. Body colorless. Segmental shoulders weak, body nearly cylindrical, shoulders reduced to level of lateral striae on segments 18–20; dorsal tubercles low, but distinct, about 20 per midbody segment; lateral striae moderate, 10–12. Body setae of anterior segments (Fig. 40) strongly clavate, becoming longer on posterior segments (Fig. 41). Anterior gonopods: median colpocoxites widely separated, gradually curving mesad, then sharply elbowed laterad, subapical spine attached to posterior margin instead of anterior (Fig. 37); lateral colpocoxites long, thin, entire (Figs. 37, 38). Telopodite process absent. Telopodites (Fig. 37) small. Posterior gonopods (Fig. 39) small, coxae deeply excavate and lobed, second articles enlarged distally, 3 distal articles reduced and fused.

Description of female paratype. Length, 14 mm, A3 = 0.87 mm. Nonsexual characters as in male. Cyphopods (Figs. 42, 43) with median valve deeply notched, lateral valve bearing a variously developed knobby bifid process.

Distribution. Known only from type locality.

Pseudotremia spira n. sp.
Figures 44–48

Types. Male holotype, female paratype, and other specimens of both sexes from Wind Cave, 5 mi. southeast of Somerset, Pulaski Co., Kentucky, collected 16 December 1956 by T. C. Barr. The specific name is an adjective meaning "spiraled."

Diagnosis. No other species in the group has the lateral colpocoxites spiraled outward in anterior view (Fig. 44).

Description of male holotype. Length, 14 mm, A3 = 1.10 mm. Ocelli 10 on each side, irregular in size, shape and arrangement (Fig. 47). Color in alcohol light brown, but probably white in life. Segmental shoulders high, angular, reduced to level of lateral striae about segment 24; dorsum nearly smooth, weak rugae beginning about segment 20, becoming stronger posteriad; lateral striae about 10. Anterior gonopods: median colpocoxite much as in *P. unca*, but lacking subapical spine (Fig. 44); lateral colpocoxites short, quite thin, spiraled in anterior view (Figs. 44, 45), entire. Telopodite process (Fig. 44) a flattened knob. Telopodites closely appressed (Fig. 44), of moderate size. Posterior gonopods (Fig. 46): similar to those of *unca*, but somewhat larger, basal knob more prominent.

Description of female paratype. Length 14–15 mm (all female specimens in fragments), A3 = 1.10 mm. Nonsexual characters as in male. Cyphopods (Fig. 48) with valves obviously fused, each valve drawn out posteriad in a pointed process.

Distribution. Known only from the type locality.

THE *EBURNEA* GROUP

This is a group of troglobites, troglophiles, and epigean species extending in a broad arc from Claiborne County, Tennessee, to adjacent parts of Alabama and Georgia and north to the Soco Gap region of North Carolina. The epigean and troglophilic species are fairly uniform; all have subapical spines on the median colpocoxites, divided lateral colpocoxites and a blunt, two-pronged telopodite process. The majority of troglobitic species of *Pseudotremia* falls in this group, primarily for reasons of geography, though in a series of species running from *P. acheron* to *P. nyx* the gonopod features named above are successively lost and the gonopods become very simple. Possibly the species of this group occurring in central Tennessee can be removed to a group of their own when more is known about the epigean species of the region, but for the time being, I believe they are best kept here.

Pseudotremia acheron n. sp.
Figures 49–52

Types. Male holotype and female paratype from Higgenbotham Cave, 8 mi. south of McMinnville, Warren Co., Tennessee, collected 23 June 1957 by L. Hubricht. The specific name is a noun in apposition, the name of one of the five rivers of Hades.

Diagnosis. Distinct from the other unpigmented troglobites of the group in having a bifurcate telopodite process, and from the troglophilic and epigean species in having a reduced number of ocelli and in lacking pigment.

Description of male holotype. Length, 16 mm, A3 = 1.00 mm. Ocelli 19 on both sides of head, irregular, unpigmented. Body without pigment. Segmental shoulders moderately strong, reduced to level of lateral striae about segment 23; dorsum smooth except for row of 8–10 strong knobs across posterior margin of each segment; lateral striae unusually prominent, 12–14. Anterior gonopods: median colpocoxite erect, simple (Fig. 48), subapical spine lacking; lateral colpocoxite (Figs. 48, 49) sigmoidally curved, divided, dorsal branch recurved, crossing over ventral, ventral branch long, sharply acuminate. Telopodite process (Fig. 48) curved slightly dorsad, deeply notched apically. Telopodites moderately large (Fig. 48), evenly rounded. Posterior gonopod (Fig. 51) typical.

Description of female paratype. Length, 18 mm, A3 = 1.04 mm. Nonsexual characters as in male. Cyphopod (Fig. 52) simple, median valve elongate, lateral valve distally widened.

Distribution. In addition to the type locality, the species is known from a male collected in McElroy Cave, 1.5 mi. northeast of Bone Cave Post Office, Van Buren Co., Tennessee, by L. Hubricht, 23 June 1957.

Pseudotremia rhadamanthus n. sp.
Figures 53–57

Types. Male holotype, female paratype, and many other specimens of both sexes from Terrill Cave, 5 mi. northeast of Guntersville, Marshall Co., Alabama, collected 2 September 1968 by S. B. Peck. The specific name is a noun in apposition, the name of one of the three judges of Hades.

Diagnosis. Differs from the other pigmented species of the group in the very large, two-pronged telopodite process and the relatively basal position of the subapical spine of the median colpocoxite.

Description of male holotype. Length, 20 mm, A3 = 1.44 mm. Ocelli 12 on each side of head, in 3 rows, regular in size and shape and well pigmented. Body pigmented as usual, light brown marked darker purplish brown. Segmental shoulders moderate, persisting to segment 25; dorsum nearly smooth on anterior segments, posterior segments with few weak rugae; lateral striae weak, 8–10. Anterior gonopods: median colpocoxite with subapical spine set about halfway in its length (Fig. 52); lateral colpocoxite curved mesad, then sharply ventrad, apically divided, divisions subequal (Figs. 52, 54). Telopodite process (Fig. 54) broad, prominent, with two widely diverging dorsally curved apices. Telopodites (Fig. 52) as usual. Posterior gonopods (Fig. 55) typical of larger pigmented species, coxae and second articles subequal, 3 apical articles of nearly equal length.

Description of female paratype. Length, 19 mm, A3 = 1.40 mm. Nonsexual characters as in male. Cyphopods (Fig. 56) ornate, lateral valve lobed, both valves with posterior processes.

Distribution. In addition to the type locality, this species is represented by specimens of both sexes from Monteagle Saltpetre Cave, southeast of Monteagle, Marion Co., Tennessee, collected by S. B. Peck, 28 August 1968. This is a considerable range for a troglobitic species of *Pseudotremia.* Caves in the intervening area should be carefully examined for this species.

Notes. The cyphopods of females from Monteagle Saltpetre Cave are slightly different from those of the paratype female (Fig. 57).

Pseudotremia soco n. sp.

Figures 58–62

Types. Male holotype from Soco Gap Falls, Jackson Co., North Carolina, collected 19 May 1956 by L. Hubricht. The specific name is a noun referring to the type locality.

Diagnosis. No other epigean species that is well pigmented has so few ocelli (14, Fig. 58). The median colpocoxites are somewhat reminiscent of *P. valga,* but bear a sinuous subapical spine.

Description of male holotype. Length, 26 mm, A3 = 1.10 mm. Ocelli 14 on each side, in 3 irregular rows (Fig. 58). Body bleached by preservation, but other specimens pigmented as usual for epigean species. Segmental shoulders very large and strong, dorsum nearly flat, reduced to level of lateral striae about segment 24; lateral striae moderately strong, 9–11. Anterior gonopods: median colpocoxites (Fig. 59) curving inward, then sharply outward, subapical spine long, slightly sinuous; lateral colpocoxites (Fig. 59, 61) extending straight ventrad, then curved sharply posteriad, divided, ventral branch the longest. Telopodite process (Fig. 60) a small knob. Telopodites as usual. Posterior gonopods (Fig. 62) typical, but apical segment somewhat elongate.

Female unknown.

Distribution. Known also from a single male collected along Rt. 197 at the Buncombe Co. line (4300 ft. elev.), North Carolina, 30 June 1955, by A. Van Pelt.

Pseudotremia eburnea Loomis

Figures 63–65

Pseudotremia eburnea Loomis, 1939, Bull. Mus. Comp. Zool., 86: 174–175, figs. 5a–c, ♂.

Types. Male holotype from Cricket Cave, Rising Fawn, Dade Co., Georgia, collected 30 August 1935 by K. Dearolf, in MCZ, examined. During a recent faunal survey of Georgia caves (S. Peck, personal communication) this cave could not be located. The specific name means "white as ivory."

Diagnosis. The telopodite process is two-parted, but small and blunt. Closest to *P. soco,* but in the holotype and most other specimens, the dorsal branch of the lateral colpocoxite is longest, and passes posteriad of the telopodites (Fig. 63), while in *soco* the ventral branch is much longer.

Description of male holotype. Length, 19 mm, A3 = 1.12 mm. Ocelli 13 on left side, 12 on right side, unpigmented, irregular in size, shape, and arrangement. Body pale tan, but fresh specimens white to pale lavender. Segmental shoulders weak, not continuing beyond segment 17; dorsum with 6–8 vague rugae, more prominent on posterior segments; lateral striae 10–12, prominent. Anterior gonopods: median colpocoxites (Fig. 63) slightly diverging, subapical spine short and stout; lateral colpocoxite divided (Figs. 63, 64), branches diverging at an obtuse angle, both curved sharply mesad. Telopodite process (Fig. 63) short, blunt, notched at distal end. Telopodites (Fig. 63) larger than usual, partly covering colpocoxites. Posterior gonopods (Fig. 65) similar to those of *P. soco,* but coxae not as prominently lobed.

Females unknown.

Distribution. Georgia: Case Caverns, at Trenton, Cloudland Canyon State Park, Dade Co., 30 September 1967, T. Iles, ♂♂. Tennessee: Nickajack Cave, Marion Co., 11 November 1967, J. Holsinger, ♂.

Pseudotremia aeacus n. sp.

Figures 66–69

Types. Male holotype and female paratype from Hurricane Cave, near Rising Fawn, Dade Co., Georgia, collected 22 October 1967 by T. Iles. The specific name is the name of one of the three judges of Hades.

Diagnosis. Close to *P. nodosa* in bearing a triangular lamella in place of the subapical spine of the median colpocoxite, but has much larger lateral colpocoxites than that species.

Description of male holotype. Length, 21 mm, A3 = 1.12 mm. Ocelli 16 on both sides, regular in shape, but irregularly arranged in 3 or 4 series. Body unpigmented. Segmental shoulders strong, high on anterior segments, dorsum nearly flat, shoulders reduced to level of lateral striae about segment 20–22; dorsum of each segment with 10–13 moderate tubercles, becoming on posterior segments row of 8 strong knobs across posterior segment margins; lateral striae weak, 7–8. Anterior gonopods: of the simplified troglobite type, median colpocoxite (Fig. 66) with a curved triangular lamella in place of subapical spine, lateral colpocoxites (Figs. 66, 67) larger than medians, entire, simply curved. Telepodite process (Fig. 67) a large, laterally flattened knob. Telopodites (Fig. 65) of moderate size. Posterior gonopods (Fig. 68) slightly reduced from those of *P. eburnea,* but similar in shape.

Description of female paratype. Length, 20 mm, A3 = 1.10 mm. Nonsexual characters as in male. Cyphopods (Fig. 69) large, obviously fused posteriorly, valves elongate.

Distribution. In addition to the type locality, known also from a single male collected in Byers Cave, 0.5 miles southwest of Hurricane Cave, 3 December 1967, by T. Iles. Hurricane Cave and Byers Cave are part of the same cave system (S. Peck, personal communication).

Pseudotremia nodosa Loomis

Figures 70–73

Pseudotremia nodosa Loomis, 1939, Bull. Mus. Comp. Zool., 86: 175–177, figs. 6a–d, ♂.

Types. Male holotype from English Cave, 0.9 mi. south of Hamilton School, Powell River, Claiborne Co., Tennessee, collected 2 July 1937 by K. Dearolf, in MCZ, examined. The specific name, meaning "knobby," is an adjective.

Diagnosis. Separated geographically from the remainder of the group, but most closely resembles *P. aeacus*, and can be separated from it by the characters mentioned under that species.

Description of male holotype. Length, about 15 mm (holotype in fragments), A3 = 0.82 mm. Ocelli 10 on right side, 11 on left side, irregular in shape and arrangement, not pigmented. Body not pigmented. Lateral shoulders almost absent, body nearly cylindrical; dorsum of each segment with 10–12 large, prominent nodules along posterior segmental margin; lateral striae weak, about 4–5 on midbody segments only. Anterior gonopods: very much simplified, median colpocoxites (Fig. 70) short, with subtriangular lamella replacing spine, lateral colpocoxites (Figs. 70–71) very short, simple, slightly curved. Telopodite process not easily observed, extending between median colpocoxites, similar in form to that of *P. aeacus*. Telopodites (Fig. 71) moderately large, curved anteriad. Right posterior gonopod (Fig. 72) similar to that of *aeacus*, but second article somewhat shorter. Left posterior gonopod missing from holotype, but Loomis (1939) shows the 3 distal articles as nearly normal for walking legs.

Description of female from English Cave. Length, 16 mm, A3 = 0.85 mm. Nonsexual characters as in male. Cyphopods (Fig. 73) with lateral valve reduced in size, median valve expanded laterad posterior to lateral valve.

Distribution. Known also from Knopper Cave, 3.3 mi. southeast of Rose Hill, Lee Co., Virginia, J. Holsinger, collector, 14 April 1968, ♂♂ ♀♀.

Notes. Except the holotype, all males examined by me had the posterior gonopods symmetrical, rather than asymmetrical, as Loomis (1939) described for the holotype.

Pseudotremia nyx n. sp.

Figures 6, 74–77

Types. Male holotype, female paratype and many other specimens of both sexes from Cathedral Caverns, 3.5 mi. north of Grant, Marshall Co., Alabama, collected 18 June 1957 by L. Hubricht. The specific name is a noun in apposition, the Greek name of the personification of darkness.

Diagnosis. The gonopods of this species resemble those of both *P. cercops* and *P. lictor*, but *P. nyx* differs from them in having 12 or more ocelli, as opposed to less than 8. In addition, *P. cercops* is almost smooth dorsally, and *P. lictor* has 12–15 strong tubercules. *Pseudotremia nyx* has 4–6 large knobs on the dorsum of each segment (Fig. 6).

Description of male holotype. Length, 19 mm, A3 = 1.00 mm. Ocelli 12 on each side, in three series, lightly pigmented. Body lacking pigment. Segmental shoulders highest in genus, raised nearly above level of dorsum, reduced to level of lateral striae on segment 28; dorsum with 4–5 strong knobs on posterior segmental margins, most median knobs raised along dorsal suture as median crest found in juveniles of most other *Pseudotremia* spp. (Fig. 6); lateral striae moderate, 6–7 per side per segment. Anterior gonopods: median colpocoxites (Fig. 74) widely separated, diverging, simple; lateral colpocoxite (Figs. 74, 75) short, simple, curved slightly ventrad. Telopodite process absent. Telopodites (Fig. 74) subequal to colpocoxites. Posterior gonopods (Fig. 75) with distal article much reduced, coxa with a large distal swelling.

Description of female paratype. Length, 19 mm; A3 = 1.00 mm. Nonsexual characters as in male, but segmental shoulders not quite so large, body more nearly cylindrical. Cyphopods (Fig. 77) extremely large for size of animal, valves swollen anteriorly, greatly drawn out and obviously fused posteriorly.

Distribution. Known only from type locality.

Pseudotremia lethe n. sp.

Figures 7, 78–80

Types. Male holotype, female paratype and a second female from Carter Cave, 3.3

mi. southwest of Flynn's Lick, Jackson Co., Tennessee, collected 21 September 1968 by J. and M. Cooper. The specific name is a noun in apposition, the name of one of the five rivers of Hades.

Diagnosis. Differing from the other highly specialized troglobitic species in the group in having the lateral colpocoxites of the gonopods branched.

Description of male holotype. Length, 13 mm, A3 = 0.70 mm. Ocelli 4 on left side, 6 on right side, irregular in shape, size and arrangement, not pigmented, barely visible. Body without pigment. Segmental shoulders moderate, reduced to level of lateral striae by segment 15; dorsum with 10–12 large, prominent tubercles on anterior segments, posterior segments with row of 12 tubercles along posterior margins; lateral striae moderate, 8 per side per segment. Anterior gonopods: median colpocoxite (Fig. 78) simple, upright, lacking a spine; lateral colpocoxite (Fig. 78) thin, extending nearly straight ventrad, branched, ventral branch much the smallest. Telopodite process absent. Telopodites (Fig. 78) moderately large. Posterior gonopods (Fig. 79) similar to those of *P. nodosa* and *P. aeacus.*

Description of female paratype. Length, 14 mm, A3 = 0.72 mm. Nonsexual characters as in male. Cyphopods (Fig. 80) like those of *P. nodosa,* but median valve more truncate, longer.

Distribution. Known only from the type locality.

Pseudotremia cercops n. sp.

Figures 81–84

Types. Male holotype from Jim Cave, 3.5 mi. east of Dowelltown, DeKalb Co., Tennessee, collected 23 December 1956 by L. Hubricht; female paratype and other females from Hill Cave, 3 mi. east of Dowelltown, collected 23 December 1956 by L. Hubricht. The specific name is a noun in apposition, the name of a kind of thieving, subterranean gnome of ancient Lydia.

Diagnosis. The male gonopods are almost indistinguishable from those of *P. lictor,* but *P. cercops* has much less prominent dorsal knobs than *P. lictor,* and the cyphopods are quite different.

Description of male holotype. Length, 13 mm, A3 = 0.90 mm. Ocelli 5 on either side, totally lacking in pigment, cuticular lenses very difficult to see. Body lacking pigment. Segmental shoulders low, reduced to level of lateral striae about segment 10; dorsum of each segment with 10–20 low, weak tubercles; lateral striae indistinct, about 10. Anterior gonopods: simplest of the genus, median colpocoxites (Fig. 81) large, erect, slightly flared, spine lacking; lateral colpocoxites (Figs. 81–82) short, entire, thin, less than half length of medians. Telopodite process absent. Telopodites (Figs. 81, 82) of moderate size. Posterior gonopods (Fig. 83) greatly reduced, coxae swollen dorsally, four distal segments all fused, reflexed dorsad; the general effect is almost that of the posterior gonopods of a species of Trichopetalidae.

Description of female paratype. Length, 13 mm, A3 = 0.92 mm. Nonsexual characters as in male. Cyphopods (Fig. 84) enormous for size of animal, greatly elongate, each valve with a short posterior process.

Distribution. In addition to the type localities, females were collected in Grant Cave, 1 mi. east of Dowelltown, DeKalb Co., Tennessee, by L. Hubricht on 23 December 1956.

Notes. It seems likely to me that *P. cercops* and *P. lictor* (described below) are descended from the same ancestor, and that this ancestor was likewise a troglobite. Assuming a roughly equal rate of evolution in the troglobitic members of *Pseudotremia,* these two species, which show the most reduction from the epigean forms, are perhaps the oldest troglobites.

Pseudotremia lictor n. sp.

Figures 85–88

Types. Male holotype, female paratype, and several other specimens of both sexes from Avant Cave, 2 mi. east of Dowelltown, DeKalb Co., Tennessee, collected 23 December 1956 by L. Hubricht. The specific name is a noun in apposition, and refers to a Roman soldier armed with a mace, suggested by the form of the posterior gonopods.

Diagnosis. Closest to *P. cercops,* but distinct from that species by the characters given under the discussion above.

Description of male holotype. Length, 14 mm, A3 = 0.95 mm. Ocelli 5 on left side, about 7 or 8 on right side, totally unpigmented, cuticular lenses hard to see. Body lacking pigment. Segmental shoulders practically absent, body roughly cylindrical; dorsum with 12–15 large, strong tubercles per segment; lateral striae moderate, 11–12. Anterior gonopods: highly simplified, much as described for *P. cercops* (Figs. 85, 86). Posterior gonopods (Fig. 87) slightly less reduced than those of *P. cercops,* but coxae much more enlarged distally.

Description of female paratype. Length, 15 mm, A3 = 0.95 mm. Nonsexual characters as in male. Cyphopods (Fig. 88) like those of *P. cercops,* but smaller, not as elongate.

Distribution. Known only from the type locality.

The *Cottus* Group

Except for *P. minos,* this group is one of the more coherent species assemblages in the genus *Pseudotremia.* All except *P. minos* are large, epigean or troglophilic species occurring in the Great Smoky Mountains, and through the foothills to the west to the area of the confluence of the Clinch and French Broad rivers. The most distinctive character linking them is the tripartite telopodite process. I think that *P. cottus, P. scrutorum,* and *P. cocytus* are definitely closely related. *Pseudotremia minos,* on the other hand, is not closely related to the other three species, but it is somewhat modified for a troglobitic existence. The form of the telopodite process (Fig. 95) is unique, but is closest to this group. The area intervening between the distribution of the three closely related species and *P. minos* has not been well collected, and perhaps other species bridging the gap between *P. minos* and the others will be found to exist there. Among the other groups, the *cottus*-group is probably most closely related to the *eburnea*-group.

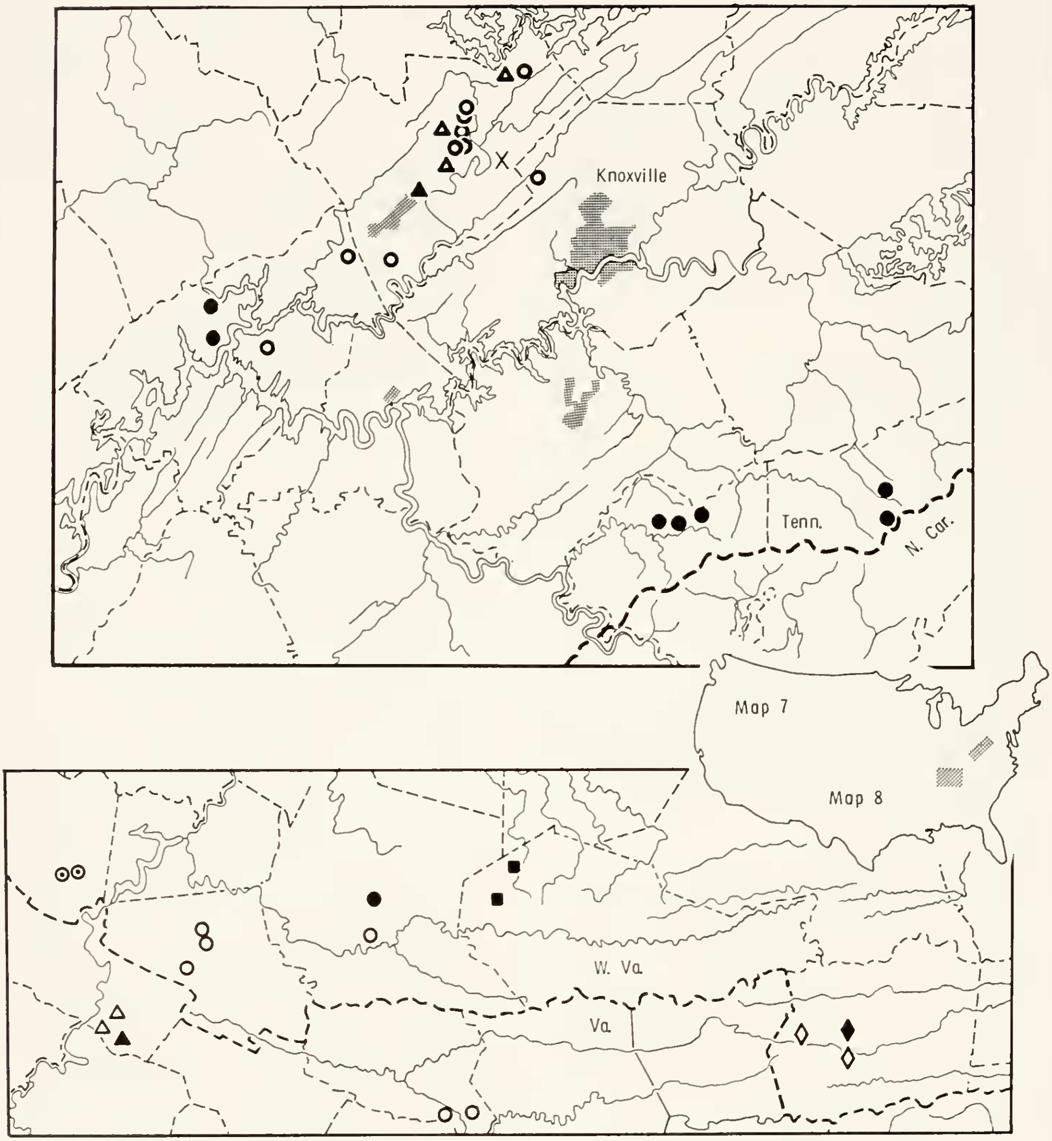
Pseudotremia scrutorum n. sp.

Figures 89–92

Types. Male holotype from trash dump, 1.7 mi. north-northeast of Winfield, Scott Co., Tennessee, collected 30 May 1958 by Leslie Hubricht. The specific name is a Latin genitive, meaning "of trash," and refers to the type locality.

Diagnosis. The lateral colpocoxites of this species are thinner than those of the others in the group (Fig. 89), and they differ further from the other two Tennessee species in the subapical spine of the median colpocoxites (Fig. 89).

Description of male holotype. Length, 28 mm, A3 = 1.45 mm. Ocelli 21 on both sides, in 5 series, regular in shape and arrangement, black. Body typically pigmented for epigean species, medium tan marked darker lavender-brown. Segmental shoulders high and prominent except on first segment and last 2 or 3 segments; dorsum with 30–40 well-defined small tubercles per segment; 8–10 moderate lateral striae. Anterior gonopods: median colpocoxites (Fig. 89) with slightly decurved subapical spine; lateral colpocoxites (Figs. 89, 90) divided, ventral branch extending straight ventrad, dorsal branch curved mesad, gland channel follows dorsal branch. Telopodite process (Fig. 90) small, bluntly 3-segmented. Telopodites (Fig. 91) as usual. Posterior gonopods



Map 7. Southwestern Tennessee, showing distribution of species of *Pseudotremia*. Solid symbols, epigean records; open symbols, cave records. Dots and circles, *P. cottus*; triangles, *P. cocytus*; cross, type locality of *P. deprehendor*.

Map 8. Eastern West Virginia and adjacent Virginia (North is to the right) showing distribution of species of *Pseudotremia*. Solid symbols, epigean records; open symbols, cave records. Dots and circles, *P. hobbsi*; circles with center dots, *P. armesi*; triangles, *P. sublevis*; squares, *P. tsuga*; diamonds, *P. simulans*.

(Fig. 92) typical of epigean species, coxa with subquadrate basal knob.

Female unknown.

Distribution. Known only from the type locality.

Pseudotremia minos n. sp.

Figures 93–97

Types. Male holotype, female paratype and other females from Russell Cave, Russell Cave National Monument, Jackson Co., Alabama, collected 10 August 1957 by D. F. Black. The specific name is the name of one of the three judges of Hades.

Diagnosis. The telopodite process is quite unique (Fig. 9); *P. minos* also differs from other species in the group in being unpigmented.

Description of male holotype. Length, 19 mm, A3 = 1.10 mm. Ocelli 21 on either side, regularly arranged in 5 series, but not pigmented. Body without pigment. Segmental shoulders high, strong, angular, dorsum nearly flat; 20–25 strong knobs and rugae per segment; 12–14 lateral striae per segment per side. Anterior gonopods: median colpocoxites (Fig. 93) with subapical spine at very tip; lateral colpocoxites very broad (Figs. 93, 94), diverging from medians high up from origin of colpocoxites, entire, evenly curved mesad. Telopodite process (Figs. 93, 95) blunt knob with 4 projections, of which central 2 are curved ventrad; median colpocoxites held *in situ* between outer and inner prongs (Fig. 94). Telopodites (Figs. 93, 94) as usual. Posterior gonopods (Fig. 96) like those of *P. scrutorum,* but basal coxal knob not as prominent.

Description of female paratype. Length 19 mm, A3 = 1.10 mm. Nonsexual characters as in male. Cyphopods (Fig. 97) with valves fused, but lateral valve recurved and overlapping central groove.

Distribution. Known only from the type locality.

Pseudotremia cocytus n. sp.

Figures 98–100, Map 7

Types. Male holotype from wooded hillside, 1.4 mi. east of Dossett, Anderson Co., Tennessee, collected 20 May 1961 by L. Hubricht. The specific name is the name of one of the five rivers of Hades.

Diagnosis. Differs from *P. scrutorum* in lacking a subapical spine on the median colpocoxite, and from *P. cottus* in the smaller, blunt telopodite process.

Description of male holotype. Length, 31 mm, A3 = 1.71 mm. Ocelli 21, regularly arranged in 5 series. Pigmentation typical of epigean species. Segmental shoulders large, strong, reduced to level of lateral striae about segment 23; dorsal tuberculation of rather weak rugae; lateral striae moderate, 9–11. Anterior gonopods: median colpocoxite (Fig. 99) short, simple, subapical spine lacking; lateral colpocoxite large, broad (Figs. 98, 99), divided, branches diverging at about a right angle (Fig. 98), sharply curved mesad, gland channel follows dorsal branch. Telopodite process (Fig. 99), like that of *P. scrutorum,* blunt, tripartite. Telopodites (Fig. 99) as usual. Posterior gonopods (Fig. 100) large, all segments apparently movable.

Females unknown.

Distribution. Besides the type locality, the following (Map 7): TENNESSEE: *Anderson Co.,* Norris Dam Cave, 2 mi. north of Norris, on logs 200 ft. from entry, 16 April 1965, J. Payne, ♂; Offutt's Cave, 2 mi. north of Clinton, 10 April 1965, J. Payne, ♂♂; 26 March 1965, J. Payne, ♂; Martin's Cave, 4 mi. southwest of Clinton, 17 April 1965, J. Payne, ♂♂, juveniles.

Note. The juvenile specimens from Martin's Cave are as follows: pigmentation light, ocelli poorly pigmented, segmental shoulders not well developed, dorsum with posterior row of large knobs on each segment, many smaller knobs anterior to these, margins of dorsal suture raised to form dorsal crest.

Pseudotremia cottus n. sp.

Figures 101–109, Map 7

Types. Male holotype and female paratype from The Sinks, Cades Cove, Blount Co., Tennessee, collected 25 May 1962 by L. Hubricht. The specific name is the name of one of the Hectanocheires, hundred-handed giants of mythology.

Diagnosis. Like *P. cocytus,* a large species, but with fewer ocelli than *P. cocytus* and with a much larger telopodite process.

Description of male holotype. Length, 30 mm, A3 = 1.72 mm. Ocelli 19 on either side, somewhat irregular in arrangement, but well pigmented. Body very dark, darker than any other species, purplish gray with darker brown markings. Segmental shoulders large, strong, reduced to level of lateral striae by segments 21–23; dorsum of each segment with 14–16 weak, elongate rugae; lateral striae prominent, 10–12 per side per segment. Anterior gonopods: median colpocoxites (Fig. 101) strong, upright, lacking subapical spine; lateral colpocoxites (Fig. 101, 102) broad, divided, gland channel follows ventral branch. Telopodite process (Figs. 103, 104) very large, tripartite, the lateral branches the largest, median colpocoxite held *in situ* between lateral branches and median projection. Telopodites normal. Posterior gonopods (Fig. 105) large, as usual for larger epigean species.

Description of female paratype. Length, 32 mm, A3 = 1.75 mm. Nonsexual characters as in male. Cyphopods (Fig. 106) with median valve slightly longer than lateral, lateral valve with broad indentation laterally.

Distribution. In addition to the type locality, the following (Map 7): TENNESSEE: *Blount Co.*, Big Poplar Trail, Cades Cove, 23 May 1962, L. Hubricht, ♂♂; near Gregory's Cave, Cades Cove, 25 May 1962, L. Hubricht, ♂; *Anderson Co.*, Marie's Cave, 1 mi. north of Andersonville, 29 May 1965, J. Payne, ♂♂, juv.; Bee Hole Cave, 4 mi. north of Clinton, 30 May 1965, J. Payne, ♂; Carden's Cave, 1 mi. northeast of Clinton, 25 January 1965, J. Payne, ♂♀♀; Wright's Cave, 2 mi. northeast of Clinton, 18 April 1965, J. Payne, ♂; Quarry No. 1 Cave, 1 mi. north of Andersonville, 29 May 1965, J. Payne, ♂♂♀; Wallace's Cave, 5 mi. north of Clinton, 4 April 1965, J. Payne, ♂♂♀♀; Melton Hill Cave, 3 mi. south of Oak Ridge, 11 April 1965, J. Payne, ♂♀♀; Community Center Cave, Norris, 16 July 1965, J. Payne, ♂♂; Spring Hill Cave, 5 mi. south of Spring Hill Community, 17 December 1965, J. Payne, ♂; *Knox Co.*, Rock Hill Cave, 2 mi. south of Heiskill, 12 June 1965, E. Mehinnick, ♂; *Roane Co.*, Eblen's Cave, near Kingston, 1 August 1955, S. Auerbach, ♂; wooded hillside 1.3 mi. southwest of Pine Grove, 1963, L. Hubricht, ♀♀; Obed River bluff at Harriman, 21 May 1961, L. Hubricht, ♀; *Sevier Co.*, west side of Indian Gap (5000 ft. elev.) 4 August 1958, R. Hoffman, ♀; between Gatlinburg and Newfound Gap, 25 May 1962, L. Hubricht, ♂.

Notes. The male gonopods show some variation. The telopodite process is much larger (Fig. 103) in the populations from Blount County, and the foothills of the Great Smoky Mountains. In the Anderson County specimens, the lateral arms are smaller (Fig. 104) and not as diverging. Among the females, there is considerable variation in cyphopod shape; the approximate range of this variation is shown in Figures 106–109.

THE *TUBERCULATA* GROUP

This group is composed of four troglophilic and epigean species from the Allegheny Plateau rim and the mountain ridges just east of it. All have divided lateral colpocoxites and a grapplelike, or divided saber type of telopodite process. There is variation, however, in the form of the subapical spine. It is absent in *P. tuberculata*, and found only as a triangular lamella in *P. armesi*. The group is closely related to the *hobbsi*-group, and the discovery of intermediate species may eventually place all *Pseudotremia* species of the northern Appalachian Valley together.

Pseudotremia tuberculata Loomis
Figures 110–113

Pseudotremia tuberculata Loomis, 1939, Bull. Mus. Comp. Zool., 86: 171–172, figs. 3a, b, ♂.

Types. Male holotype from Cassel Farm Cave, Burkes Garden, Tazewell Co., Virginia, collected 3 July 1937 by K. Dearolf, in MCZ, examined. The specific name refers to the body texture.

Diagnosis. The extremely long ventral branch of the divided lateral colpocoxite (Fig. 110) sets *P. tuberculata* off from any other species.

Description of male from type locality. Since the holotype is in poor condition, a male collected at the type locality by R. L. Hoffman, 27 June 1947, is described here. Length, 29 mm, A3 = 1.35 mm. Ocelli 18 on both sides of head, somewhat irregular in form and arrangement, not fully pigmented. Coloration as usual, light tan-brown marked darker purplish brown. Segmental shoulders moderate, reduced to level of lateral striae about segment 21–23; dorsal tuberculation very strong, large, discrete tubercles densely scattered over midbody segments; lateral striae very strong, 12–14. Anterior gonopods: median colpocoxites (Figs. 110, 111) divided, ventral branch much the longest and thinnest, arching straight ventrad. Telopodite process (Fig. 110) grapplelike, base shaped like a gear wheel. Telopodites (Figs. 110, 111) of moderate size. Posterior gonopods (Fig. 112) typical of larger species.

Description of female from type locality. Length, 30 mm, A3 = 1.37 mm. Nonsexual characters as in male. Cyphopods (Fig. 113) large, valves thick, median valve the longest.

Distribution. Known only from the type locality.

Pseudotremia momus n. sp.
Figures 114–117

Types. Male holotype, female paratype and other specimens of both sexes from Spence Cave, between Saltville and Chatham, Smyth Co., Virginia, collected 3 January 1956 by R. L. Hoffman. The specific name is the name of the Roman god of ridicule, suggested by the peculiar form of the median colpocoxites.

Diagnosis. The form of the median colpocoxites in lateral view (Fig. 115) is distinctive.

Description of male holotype. Length, 23 mm, A3 = 1.26 mm. Ocelli 17 on both sides, in 4 or 5 series, regular in shape, black. Pigmentation typical of epigean and large troglophilic species. Segmental shoulders strong on every segment but penultimate and anal; dorsum of each segment with a few low rugae, becoming posterior row of 10–12 moderate tubercles on posterior segments; lateral striae moderate, 10–12. Anterior gonopods: median colpocoxites broad in anterior view (Fig. 114), subapical spine hooklike, in lateral view median colpocoxite (Fig. 115) sharply decurved, almost forming a circle; lateral colpocoxites small (Fig. 115) short, divided at apex. Telopodite process (Fig. 114) grapplelike, base swollen and resembling a gear wheel. Telopodites as usual. Posterior gonopods (Fig. 116) normal for epigean or troglophilic species.

Description of female paratype. Length, 25 mm, A3 = 1.25 mm. Nonsexual characters as in male. Cyphopods (Fig. 117) smaller than in *P. tuberculata,* lateral valves with a few vague lobes.

Distribution. Besides the type locality, a male was collected on the crest of Big Walker Mt., 4 mi. south of Ceres, Wythe and Bland Co., Virginia, 1 June 1969, by R. L. Hoffman.

Pseudotremia armesi n. sp.
Figures 118–121, Map 8

Types. Male holotype, female paratype, and other specimens of both sexes from Neely Farm Cave,[1] Athens, Mercer Co., West Virginia, collected 13 February 1966 by W. Shear and B. W. Armes. The specific name is in memory of my friend and student, B. W. Armes, who helped in the collection of the type series, and whose promising scientific career was cut short in Viet Nam.

---

[1] This cave has been variously known as Barrett Cave, Bear Cave, Theta Xi Cave, etc., but will appear under this name in the forthcoming *Caves of West Virginia* (J. Holsinger, personal communication).

Diagnosis. The triangular lamella in place of a subapical spine of the median colpocoxites distinguishes this species from any others of the group.

Description of male holotype. Length, 22 mm, A3 = 1.26 mm. Ocelli 19 on either side, slightly irregular in size, irregular in arrangement, poorly pigmented. Body pale brown, vaguely marked darker, especially on anterior segments. Segmental shoulders moderate, reduced to level of lateral striae about segment 25; dorsum of each segment with a few moderately prominent rugae; lateral striae weak, about 8 per side per segment. Anterior gonopods: median colpocoxites upright, triangular lamella in place of subapical spine (Fig. 118); lateral colpocoxites divided (Figs. 118, 119), ventral branch sharply curved dorsad. Telopodite process (Fig. 118) grapplelike, lacking gear-wheel base seen in *P. tuberculata* and *P. momus.* Telopodites as usual. Posterior gonopods (Fig. 120) with second article slightly longer than coxae.

Description of female paratype. Length, 23 mm, A3 = 1.22 mm. Nonsexual characters as in male. Cyphopods (Fig. 121) as in *P. momus,* but median valve somewhat longer in comparison to lateral.

Distribution (See Map 8). Besides the type locality, three females were collected near Brush Creek Falls, 3 mi. northeast of Princeton, Mercer Co., West Virginia, 15 June 1967, by W. A. Shear. The type locality is a small cave in a thin band of Hinton limestone, and is isolated by about 20 miles from any other caves.

Pseudotremia alecto n. sp.

Figures 122–124

Types. Male holotype and a second male from Griffith, Alleghany Co., Virginia, collected 6 May 1950 by R. Hoffman and L. Hubricht. The specific name is the name of one of the Furies of Greek mythology.

Diagnosis. The unusual clasplike form of the median colpocoxites (Fig. 122) is found only in *P. simulans* and *P. alecto; simulans* occurs in Pendleton Co., W. Va. and is much larger (*ca.* 30 mm) than *alecto* (*ca.* 25 mm).

Description of male holotype. Length, 26 mm, A3 = 1.17 mm. Ocelli 19 on both sides of head, arranged in 5 series, pigmented. Coloration typical of epigean species. Segmental shoulders moderately high, reduced to level of lateral striae about segment 20–22; dorsal tuberculation very well developed, nearly 50 small but distinct tubercles on dorsum of each midbody segment; lateral striae prominent, 16–18. Anterior gonopods: median colpocoxites (Fig. 122) somewhat resembling those of *P. valga* and *P. soco,* but subapical spine forming forcepslike arrangement with a projection from the tip of median colpocoxite; lateral colpocoxites (Figs. 122, 123) broad, evenly curved, apically divided. Telopodite process (Fig. 123) short, thin, apically notched. Telopodites as usual. Posterior gonopods (Fig. 124) typical of larger species.

Females unknown.

Distribution. Known only from the type locality.

THE *HOBBSI* GROUP

This is a large, complex, heterogeneous group of epigean and troglophilic species (*P. fulgida* and *P. lusciosa,* included here, are the only troglobites) from the northern part of the range of *Pseudotremia,* though *P. deprehendor* is found far to the south in Tennessee. The absence of records from southwestern Virginia precludes any statement about the relationship of *P. deprehendor* to the rest of the group; a large collection from the area exists, but was not available for this study. The parts of West Virginia and Kentucky intervening between the distribution of most species of the group and *P. carterensis* are difficult to get to and have not been well collected. There are two large female specimens of an undescribed species from Clay County, West Virginia (Map 5). The group seems related to the *tuberculata*-group, but also has affinities with the similarly northern *indianae*-group. Most of the species included in the *hobbsi*-group have a subapical spine on the median colpocoxite. The lateral colpocoxite may be divided or not, and the telopodite process, when present, is of the saberlike type.

Pseudotremia lusciosa (Loomis)
Figures 125–127

Dearolfia lusciosa Loomis, 1939, Bull. Mus. Comp. Zool., 86: 178–179, figs. 7a–f, ♂.

Types. Male holotype from Seneca Caverns, 3 mi. northeast of Riverton, Pendleton Co., West Virginia, collected 1 June 1935 by K. Dearolf, in MCZ, examined. The specific name is a Latin adjective, meaning "partly blind."

Diagnosis. The median colpocoxites are fused together for a considerable distance from their bases (Fig. 125); the gonopods of no other *Pseudotremia* species are known to be of this form. The superficial resemblance to species of *Cleidogona* led Loomis (1939) to erect the supposedly intermediate genus *Dearolfia*.

Description of male holotype. Length, 17 mm, A3 = 1.25 mm. Ocelli 7 on right side, 5 on left, small and unpigmented. Body without pigment. Segmental shoulders moderate, reduced to level of lateral striae about 17–19; dorsum nearly smooth, only a few vague rugae on midbody segments; lateral striae strong, 7–8 per side per segment. Anterior gonopods: median colpocoxites (Fig. 125) fused to each other for more than half their length, subapical spine erect; lateral colpocoxites (Fig. 126) long, thin, entire, evenly curved. Telopodite process not visible in figures, but of short saberlike form. Telopodites (Figs. 125, 126) smaller than usual. Posterior gonopods (Fig. 127) more reduced than in other members of the group, with deeply excavate coxae.

Females unknown. Loomis (1939) reported having a female, but it could not be located.

Distribution. Known only from the type locality.

Pseudotremia simulans Loomis
Figures 128–134, Map 8

Pseudotremia simulans Loomis, 1939, Bull. Mus. Comp. Zool., 86: 170–171, figs. 2a–b, ♂.

Types. Male holotype from Simmons Cave, near Cave Post Office, Pendleton Co., West Virginia, collected 5 July 1937 by K. Dearolf, in MCZ, examined. The specific means "simulating," or "imitating," and refers to the resemblance of this species to *P. princeps*, of the same region.

Diagnosis. The forcepslike arrangement at the apex of the median colpocoxite separates this species from all *Pseudotremia* except *P. alecto*, which is a smaller species.

Description of male from Trout Cave, 3 mi. south of Franklin. The description is taken from this specimen, which I compared with the type, since the holotype is in poor condition. Length, 32 mm, A3 = 1.60 mm. Ocelli 20, in 5 series, black. Pigmentation typical of larger species. Segmental shoulders strong, dorsum nearly flat, shoulders obvious to penultimate segment; dorsum with a few weak rugae, mostly on posterior margins of midbody segments; lateral striae moderate, 12–14. Anterior gonopods (Fig. 129): median colpocoxites with subapical spine; lateral colpocoxites (Fig. 132) simple, entire, curved abruptly ventrad. Telopodite process absent. Telopodites somewhat larger than usual. Posterior gonopods (Fig. 131) somewhat more complexly knobbed at base of coxae than in other large species.

Description of female from Trout Cave. Length, 31 mm, A3 = 1.60 mm. Nonsexual characters as in male. Cyphopods (Fig. 134) with lateral valve much the largest, broader than long.

Distribution. In addition to the type locality, the following (Map 8): West Virginia: *Pendleton Co.*, Trout Cave, 3 mi. south of Franklin, 15 October 1950, R. Johnson, ♂♂♀♀; marsh 3 mi. west of Franklin, 22 May 1958, L. Hubricht, ♂.

Notes. The male from 3 mi. west of

Franklin differs in the general appearance of the gonopods, and has more ocelli (24) than the male holotype or males from Trout Cave. Because of these differences, the gonopods of the specimen are fully illustrated in Figures 128–130. This specimen may represent an undescribed species close to *P. simulans*, but because of the many similarities, I am reluctant to describe it as such from a single male.

Pseudotremia fulgida Loomis
Figures 135–140, Map 8

Pseudotremia fulgida, Loomis, 1943, Bull. Mus. Comp. Zool., 92: 378–380, figs. 3a–d, ♂.

Types. Male holotype from Higgenbotham Cave, 1.5 miles northwest of Frankford, Greenbriar Co., West Virginia, collected 24 August 1939 by L. Hubricht. The specific name is a Latin adjective meaning "shining."

Diagnosis. No other species has such a large, prominent, saberlike telopodite process (Figs. 135, 136).

Description of male holotype. Length, 18 mm, A3 = 1.05 mm. Ocelli 7 on either side, irregularly arranged, lightly pigmented. Body without pigmentation. Segmental shoulders moderate, reduced to level of lateral striae by segment 15–17; dorsum nearly smooth, only posterior segments with few low rugae; lateral striae 8–10, moderate. Anterior gonopods: median colpocoxite (Fig. 135) simple, bladelike, erect, lacking subapical spine; lateral colpocoxites (Figs. 135, 136) broad, simple, entire, evenly curved. Telopodite process (Figs. 135, 136) very large, saberlike, curved in two-thirds of a circle between colpocoxites. Telopodites (Fig. 136) somewhat smaller than usual. Posterior gonopods (Fig. 137) somewhat like those of larger, epigean species, but coxa more swollen distally.

Description of female from type locality. Length, 19 mm, A3 = 1.08 mm. Nonsexual characters as in male. Cyphopods (Figs. 138–140) showing some variation in specimens from type locality, but generally with lateral valve subquadrate, median valve slightly elongated, distally flattened.

Distribution. In addition to the type locality, the following: WEST VIRGINIA: *Greenbriar Co.*, Hayes Cave, 5 mi. north of Lewisburg, 12 August 1939, L. Hubricht, ♀; Coffman Cave, near Frankford, 11 April 1967, T. C. Barr, ♂♂♀♀; Poor Farm Cave, 1.5 mi. east of Williamsburg, 27 September 1969, J. Holsinger, ♂.

Notes. Coffman Cave is part of the Higgenbotham Cave System, which includes three caves under the name Higgenbotham Cave (numbered one to three; Davies, 1949). *Pseudotremia hobbsi* also occurs in or near this cave system.

Pseudotremia carterensis Packard
Figures 141–144

Pseudotremia cavernarum carterensis Packard, 1883, Proc. Amer. Philos. Soc., 21: 186.

Pseudotremia carterensis, Cook and Collins, 1895, Ann. New York Acad. Sci., 9: 40, figs. 8–10, ♂.

Pseudotremia sodalis Loomis, 1939, Bull. Mus. Comp. Zool., 86: 173–174, figs. 4a–d, ♂. NEW SYNONYMY.

Types. Syntypes of *P. carterensis* from Bat Cave, Carter's Cave, Zwingell's Cave and X Cave, Carter Caves, Carter Co., Kentucky. Zwingell's Cave specimens collected 13 September 1874 by T. Sanborne, others without date or collector's name, in MCZ, examined; male holotype of *P. sodalis* from Bat Cave, Carter Caves, Carter Co., Kentucky, collected 25 June 1937 by K. Dearolf, in MCZ, examined; gonopods missing from vial.

Diagnosis. The small size of the subapical spine and the presence of a small tooth on the lateral colpocoxite (Fig. 141) are distinctive.

Description of male from Bat Cave. Length, 18 mm, A3 = 1.07 mm. Ocelli 20 on both sides, in 4 series, regular and well pigmented. Body pigmented as usual for epigean and troglophilic species. Segmental shoulders low to moderate; reduced to level of lateral striae on segments 20–22; dorsum nearly smooth anteriorly, with a few low rugae on midbody segments, becoming moderately well-defined elongate tubercles on posterior body segments; lateral striae moderately strong, 10–12. Anterior gonopods: median colpocoxite (Fig. 141) with subapical spine small but distinct; lateral colpocoxite (Fig. 141, 142) not divided, short, broad, evenly curved, with a small ventral tooth in most specimens. Telopodite process (Fig. 141) short, of the saberlike type. Telopodites (Fig. 141) quite large, curving forward. Posterior gonopods (Fig. 143) with coxal base somewhat more knobby than usual.

Description of female from Bat Cave. Length, 19.5 mm, A3 = 1.10 mm. Nonsexual characters as in male. Cyphopods (Fig. 144) with lateral valve bearing an anterior flange, both valves elongate, median valve slightly longer.

Distribution. Known only from the caves listed above, Carter Co., Kentucky. The record of a female from a rotted stump in Adams Co., Ohio (Williams and Hefner, 1928), has not been confirmed.

Notes. This species has been the subject of considerable confusion. Though Packard (1883) did not formally designate types, a series of specimens from the same caves he listed was found in the general collection in the MCZ, with labels in handwriting similar to that on the labels of other Packard specimens, and marked as "paratypes."[1] Included was a single male, labelled as being from Carter's Cave. The holotype male of *P. sodalis* Loomis, from Bat Cave, lacks gonopods. I compared the male from the Packard series with a collection of three males made in Bat Cave by T. C. Barr on 27 May 1957, and found agreement in all respects, except that the Packard specimen had each subapical spine double. In the absence of any other such specimen, I prefer to regard this as an anomaly.

The confusion is deepened by Cook and Collins' (1895) statement that their description of *P. carterensis,* which fits Packard's specimens quite well, was drawn from material collected in Wyandotte Cave, Indiana, where only *P. indianae* Chamberlin and Hoffman is known to occur. It was implied that C. H. Bollman collected this material. It seems likely that it was mislabelled; nothing like *P. carterensis* has been collected in Indiana since.

Pseudotremia deprehendor n. sp.

Figures 145–147, Map 7

Types. Male holotype and a second male collected in Feather's Cave, 4 mi. east of Clinton, 2 August 1965 by J. Payne. The specific name is a noun in apposition and means "one who takes by surprise."

Diagnosis. The telopodite process is a long, double saber (Fig. 145), which also occurs in *P. merops*, but *merops* has only 12 ocelli while *P. deprehendor* has 20 or more.

Description of male holotype. Length, 21 mm, A3 = 1.25 mm. Ocelli 21 in 4 or 5 irregular series, well pigmented. Body pigmented as usual, light brown marked darker purplish brown. Segmental shoulders low, reduced to level of lateral striae about segment 23; dorsum with numerous low, elongate tubercles; lateral striae prominent, 10–12. Anterior gonopods: median colpocoxite (Fig. 145) with very long, slightly sinuous subapical spine; lateral colpocoxites (Figs. 145, 146) thin, rather small, spirally curved when seen in anterior view (Fig. 145) but curved inward, not outward as in *P. spira.* Telopodite process (Fig. 145) long, curved double saber type, curved through about one half of a circle. Telopodites small. Posterior gonopod (Fig. 147) with coxa quite flattened, two prominent mesal notches, second article expanded distally.

Female unknown.

Distribution. Known only from the type locality (Map 7). The occurrence of this species in Anderson Co., Tennessee, in the midst of the distributions of *P. cottus* and *P. cocytus,* two species that are closely related to each other but not at all to *P.*

---

[1] These may have been so marked by R. V. Chamberlin.

deprehendor, is remarkable. *P. deprehendor* also shows some affinities with the *spira*-group.

Pseudotremia princeps Loomis
Figures 148–151

Pseudotremia princeps Loomis, 1939, Bull. Mus. Comp. Zool., 86: 168–170, figs. 1a–c, ♂.

Types. Male holotype from Eagle Cave, West Virginia, collected 22 April 1935 by K. Dearolf, in MCZ, examined.

The only Eagle Cave listed in *Caverns of West Virginia* (Davies, 1949: 163) is in Monongalia County, about 100 miles northwest of all other known localities for *P. princeps,* and is developed in the Greenbriar Limestone (Mississippian). The other localities are all in the Coeymans Limestone (Ordovician-Silurian) in Pendleton County. Neither Loomis (1939) nor Dearolf (1937) gives any details about the location of "Eagle Cave," and it seems likely to me that this name actually refers to an unlisted cave in Pendleton County. There is an Eagle Rock in Pendleton County. Such a wide distribution of a *Pseudotremia* species would be unique. The specific name means "largest" or "principal."

Diagnosis. A very large (30–36 mm long) species, *P. princeps* can be distinguished from its closest relatives (*P. simulans* and *P. tsuga*) by the basally very broad lateral colpocoxites (Fig. 146) divided into two large branches.

Description of male from Mystic Cave. Length, 32 mm, A3 = 1.70 mm. Ocelli 22 on both sides, in 5 or 6 series, well pigmented. Body with pigmentation typical of large epigean species. Segmental shoulders strong, dorsum of anterior segments nearly flat, reduced to level of lateral striae by segment 20–22; dorsum with a few weak rugae on midbody segments; lateral striae 14–17, moderate. Anterior gonopods: median colpocoxites (Fig. 148) rather small, subapical spine short, straight; lateral colpocoxites (Figs. 148, 149) very broad at the base, divided, branches unequal, dorsal branch much the longest. Telopodite process (Fig. 149) a low, flattened swelling. Telopodites (Fig. 148) large and broad. Posterior gonopods (Fig. 150) as usual.

Description of female from Mystic Cave. Length, 37 mm, A3 = 1.72 mm. Nonsexual characters as in male. Cyphopods (Fig. 151) simple, valves distally flattened, lateral valve broader, shorter, than median valve.

Distribution. In addition to the type locality the following: West Virginia: *Pendleton Co.,* Smoke Hole Cave, 1.1 mi. south of Branch, Pendleton Co., 20 April 1935, K. Dearolf, ♂♂ (Loomis, 1939); Mystic Cave, 0.4 mi. southwest of Teterton, 30 May 1952, L. Hubricht, ♂♀; east side of North Fork, 3.5 mi. southeast of Riverton, 22 May 1958, L. Hubricht, ♂.

Pseudotremia tsuga n. sp.
Figures 152–156, Map 8

Types. Male holotype and another male from Cranberry Glades Natural Area, near Mill Point, Monongahela National Forest, Pocahontas Co., West Virginia, collected 20 May 1967 by W. A. Shear and Paul Vogel; female paratype and another female from a marsh, Mill Point, Pocahontas Co., West Virginia, collected 23 May 1958 by L. Hubricht. The specific name is the generic name of the hemlock, and refers to the habitat of the holotype, a dense bog forest of hemlock.

Diagnosis. The small, recurved, ventral branch of the lateral colpocoxites (Fig. 150) and the short, saberlike telopodite process sets this species apart from the others of the group.

Description of male holotype. Length, 35 mm, A3 = 1.53 mm. Ocelli 25 in 6 series, well pigmented. Body pigmentation as usual in large epigean species. Segmental shoulders strong, high, similar to those of *P. princeps;* dorsum with a few weak, elongate tubercles strongest on midbody segments; lateral striae 9–12, moderate. Anterior gonopods: median colpocoxites

(Fig. 152) short, slightly divergent, subapical spine curved dorsad; lateral colpocoxites (Figs. 152, 153) divided, ventral branch short, slender, recurved. Telopodite process (Fig. 153) of the short saberlike type. Telopodites (Fig. 154) slightly smaller than in *P. princeps.* Posterior gonopods (Fig. 155) similar to those of *P. princeps,* but slightly smaller.

Description of female paratype. Length, 30 mm, A3 = 1.50 mm. Nonsexual characters as in male. Cyphopods (Fig. 156) somewhat like those of *P. princeps,* but more irregular in outline.

Distribution. Known only from type localities (Map 8). Core (1955) has described the unusual relict area of Cranberry Glades. Barr (1967) found a species of the otherwise troglobitic carabid beetle genus *Pseudanophthalmus* on the surface at Cranberry Glades, many miles from any cavernous limestone. I have collected the boreal xystodesmid milliped *Semoniellus placidus* (Wood) nearby, the only West Virginia record; Hoffman (1969a) reports that *S. placidus* occurs primarily in the northern midwest, with a relict population in Virginia on high mountains.

Pseudotremia cavernarum Cope
Figures 157–160

Pseudotremia cavernarum Cope, 1869 (not Cook and Collins, 1895), Proc. Amer. Philos. Soc., 11: 179; Hoffman, 1958, Proc. Biol. Soc. Washington, 71: 113–118, figs. 1, 2, ♂.

Types. Type specimens collected by E. D. Cope in Erhart's Cave, 3 mi. southeast of Blacksburg, Montgomery Co., Virginia, believed destroyed.

Diagnosis. Distinguished from *P. hobbsi* by the much shorter subapical spines of the median colpocoxites in *P. cavernarum* (Fig. 157).

Description of male from Erhart's Cave. Length, 20 mm, A3 = 1.05 mm. Ocelli 15, irregularly arranged, weakly pigmented. Body light translucent brown. Segmental shoulders weak, body nearly cylindrical; dorsal surface smooth on anterior segments, posterior segments with row of small tubercles on posterior margins; lateral striae prominent, 12–14. Anterior gonopods: median colpocoxites erect (Fig. 157), divided, ventral branch much the longest. Telopodite process (Fig. 158) of the short saberlike type. Telopodites (Fig. 157) large. Posterior gonopods (Fig. 159) as usual.

Description of female from Erhart's Cave. Length, 21 mm, A3 = 1.00 mm. Nonsexual characters as in male. Cyphopods as in Figure 160.

Distribution. Known only from the type locality.

Notes. Before genitalic characters were widely used to distinguish species of millipeds, *Pseudotremia* was considered to contain only the single species, *P. cavernarum*; thus pre-1939 published records of this species are not reliable. Cook and Collins (1895) wrote their description of *P. cavernarum* from specimens collected in Wyandotte Cave, Indiana; Chamberlin and Hoffman (1958) provided the new name *P. indianae* for this material. It was not until 1958 that R. L. Hoffman published a detailed description of specimens collected at the type locality, the only place where *P. cavernarum* is known to occur. I visited the type locality in April, 1969, in company with Hoffman. Quarrying operations had blocked off the cave about 30 m from the entrance, and have since probably destroyed it completely.

Pseudotremia hobbsi Hoffman
Figures 1–5, 161–167, Map 8

Pseudotremia hobbsi Hoffman, 1950, J. Washington Acad. Sci., 40: 90–91, figs. 5, 6, ♂.

Types. Male holotype and many paratypes of both sexes from Chestnut Ridge Cave. 2 mi. north of Clifton Forge, Alleghany Co., Virginia, collected 31 March 1947 by R. L. Hoffman, in USNM, examined.

Diagnosis. Distinct from all other species of *Pseudotremia* in the unusually long subapical spine of the median colpocoxite (Figs. 161, 162).

Description of male holotype. Length, 30 mm, A3 = 1.47 mm. Ocelli 19 on left side, 20 on right side, arranged in 5 series, pigmented. Body with typical pigmentation. Segmental shoulders strong, reduced to level of lateral striae about segment 20; dorsum moderately rough, 12–20 elongate tubercles on posterior portions of midbody segments; lateral striae rather weak, 14–16. Anterior gonopods: median colpocoxite (Fig. 159) with subapical spine as long as colpocoxite, erect; lateral colpocoxite not divided or with a small tooth (Fig. 160). Telopodite process of the saber type, moderately long (Fig. 161). Telopodites as usual. Posterior gonopods (Fig. 164) typical of larger species.

Description of female paratype. Length, 30 mm, A3 = 1.45 mm. Nonsexual characters as in male. Cyphopods (Fig. 167) similar to those of *P. cavernarum.*

Distribution. In addition to the type locality, the following (Map 8): VIRGINIA: *Alleghany Co.*, Quarry Cave at Lowmoor, 3 March 1948, R. Hoffman, ♂; Warm Springs Mountain, elev. 3600 ft., no date, L. Hubricht, ♂; *Montgomery Co.*, Slusser's Chapel Cave, 2 mi. northeast of Slusser's Chapel, 21 April 1968, J. Holsinger, ♂. WEST VIRGINIA: *Greenbriar Co.*, near Coffman Cave, 1.7 mi. west-southwest of Frankford, 11 April 1957, T. C. Barr, ♂♀♀; Higgenbotham Cave, 1.3 mi. west of Frankford, 11 April 1957, T. C. Barr, ♂♂; Dry Run Cave, 1.5 mi. west-northwest of Sunlight, 27 January 1968, J. Holsinger and R. Baroody, ♂; *Monroe Co.*, Greenville Saltpetre Cave, 0.4 mi. northeast of Greenville, 10 April 1969, W. A. Shear, L. Bayless, and N. Tuggle, ♂♂♀♀; Laurel Creek Cave, 1.5 mi. northeast of Greenville, 10 April 1969, W. A. Shear, L. Bayless, and N. Tuggle, ♂♂♀♀; Rock Camp Cave, 1.9 mi. southeast of Rock Camp, 1 July 1968, T. C. Barr, ♂♂.

Notes. Both this species and *P. cottus* have the most extensive known ranges of epigean and troglophilic species of *Pseudotremia,* and as in *P. cottus,* there is variability in the gonopods of *P. hobbsi.* Figures 163–165 show the variation in branching of the lateral colpocoxite in West Virginia (Greenbriar Valley) specimens. Virginia (James River drainage) specimens, and the types, have the colpocoxite unbranched (Figs. 161, 162). A detailed study of the variation awaits the collection of large samples from localities throughout the range of the species.

Pseudotremia sublevis Loomis
Figures 168–172, Map 8

Pseudotremia sublevis Loomis, 1944, Psyche, 51: 167–168, figs. 1A–C, ♂.

Types. Male holotype from Tony's (Tawney's) Cave, 8 mi. east of Pearisburg, Giles Co., Virginia, collected 9 May 1943 by H. W. Jackson, in MCZ, examined. The specific name means "lifted" or "supported."

Diagnosis. The small median colpocoxites in combination with the very large, L-shaped ventral branches of the lateral colpocoxites (Fig. 168) are unique.

Description of male holotype. Length, 28 mm. A3 = 1.45 mm. Ocelli 19, in 6 series, well pigmented. Body with the usual pigmentation. Segmental shoulders moderate, reduced to level of lateral striae about segment 20–22; dorsum as in *P. cavernarum,* nearly smooth; lateral striae 15–17, prominent. Anterior gonopods: median colpocoxites (Figs. 168, 169) small, short, simple, subapical spine lacking; lateral colpocoxites divided (Fig. 168), ventral branch enlarged, L-shaped, extending straight ventrad, gland channel following dorsal branch, which curves evenly mesad. Telopodite process (Fig. 168) of the short, saberlike type, with a large knob at the base. Telopodites as usual. Posterior gonopods (Fig. 170) typical of larger species.

Females unknown.

Distribution. In addition to the type locality, the following: VIRGINIA: *Giles Co.,* Spruce Run Mountain Cave, 0.5 mi. south of Maybrook (Hoffman, 1958); sinkhole 5 mi. west of Newport, 16 June 1962, R. Hoffman, ♂; *Montgomery Co.*, Dry Run, 5 mi. east of Blacksburg, 10 April 1969, W. Shear, R. Hoffman, L. Knight, ♂.

Notes. The specimen from the sinkhole near Newport differs from the holotype in the form of the ventral branch of the lateral colpocoxite; compare Figures 171 and 172.

Genus *Solaenogona* Hoffman

Solaenogona Hoffman, 1950, J. Washington Acad. Sci., 40: 91; Loomis, 1968, U. S. Nat. Mus. Bull., 266: 69 (list).

Type species. Solaenogona guatemalana Hoffman, by original designation. The generic name is a feminine Latin neologism, and indicates relationship to the genus *Cleidogona*, and the grooved branch (solenomerite) of the gonopods.

Diagnosis. The enormous processes developed from the posterior surfaces of the colpocoxites of the anterior gonopods and the much reduced telopodites distinguish this genus from the others of the Cleidogonidae.

Description. Thirty segments. Mentum divided. Antennae moderately long, shorter than in *Pseudotremia.* Ocelli always present. Body fusiform, evenly tapering posteriad in males from segment 7. Segments cylindrical, segmental setae short, acuminate. Surface of segments smooth, without lateral striations. Pregonopodal legs of males: legs 1 and 2 6-segmented, reduced slightly in size. Legs 3 through 7 much enlarged, crassate, tarsi with special setae. Anterior gonopods (Figs. 173, 177): very large and prominent, colpocoxites apically complex, with lateral emarginations and several apical processes, posteriorly with a large, heavy process curving ventrad to meet tip of colpocoxite. Telopodites basally fused, not movable, small. Posterior gonopods (Fig. 175): sternum bandlike, weakly sclerotized. Usually with 5 or 6 segments, coxae enlarged, not conspicuously lobed, remnants of coxal sacs near base of coxae; second segment sometimes not distinctly set off from coxa, elongate, roughly cylindrical; third segment similar to second, always distinct; 3 distal segments usually fused; claw present or absent. Cyphopods (Figs. 176, 180): typical of the family, postgenital plate present, of various forms.

Distribution. Highlands of western Guatemala and adjacent Chiapas, Mexico; Map 9.

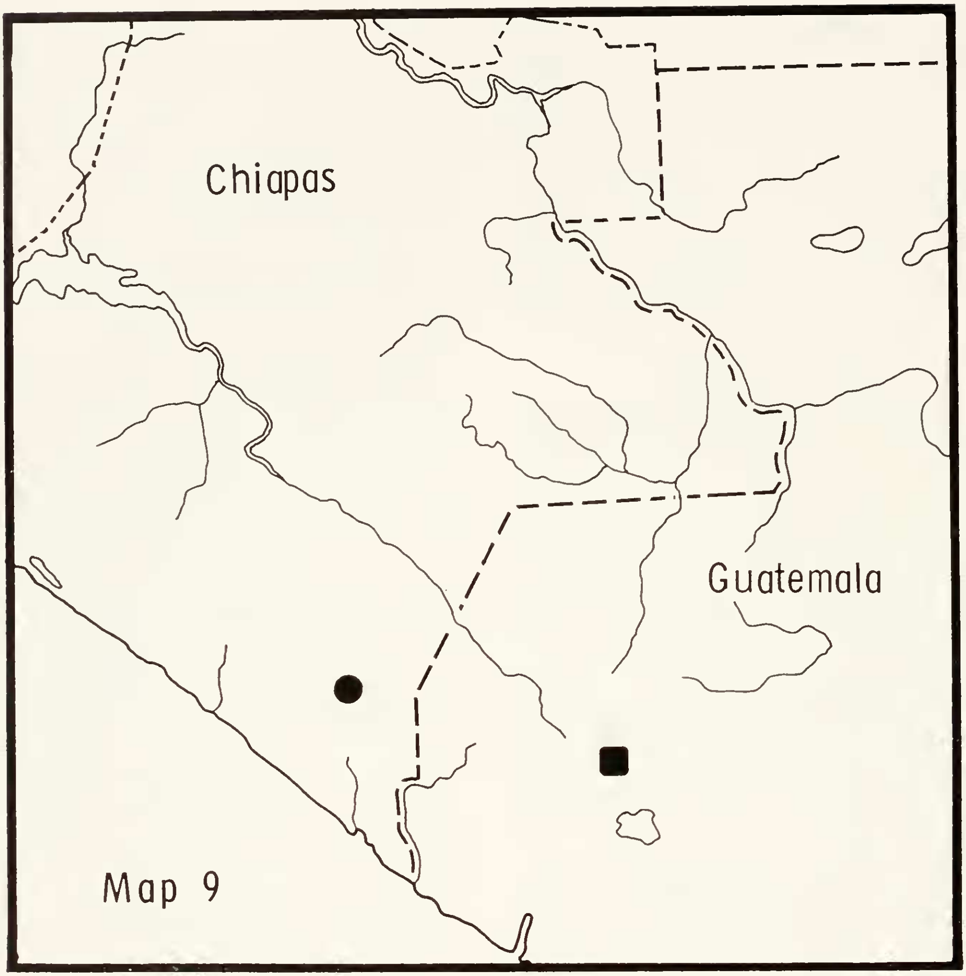
Notes. This genus is a particularly significant one from an evolutionary standpoint, since it combines some of the characters of *Pseudotremia* and *Cleidogona.* The present limited range of *Solaenogona* near the southern periphery of the range of the family seems to indicate a less progressive, perhaps primitive form now restricted in its distribution by competition from the more highly adapted species of *Cleidogona* occurring in southern Mexico. It seems likely that *Solaenogona* was derived from the same ancestral stock as *Pseudotremia,* but at a slightly later time, when some changes toward a *Cleidogona*-like form had already taken place. See the section above on generic relationships.

There are analogies (homologies?) in the gonopods of *Solaenogona* and *Pseudotremia.* The grooved colpocoxite of *Solaenogona* may correspond to the lateral colpocoxite of *Pseudotremia,* and *Solaenogona*'s massive posterior colpocoxite process, which has a fringed tip and probably functions in spermatophore transfer, may be homologous to the median colpocoxite of *Pseudotremia.*

KEY TO SPECIES OF *SOLAENOGONA*

1a. Apical spine of colpocoxite of gonopods (Fig. 173) acuminate; postgenital plate of females without a median shieldlike part (Fig. 176) .... *guatemalana*

1b. Apical spine of colpocoxite of gonopods (Fig. 177) with an expanded plate at the tip; postgenital plate of females with a median shield (Fig. 180) .... *chiapas*



Map 9. Chiapas, Mexico, and western Guatemala, showing distribution of species of the genus *Solaenogona*. Dot, type locality of *S. chiapas*; square, type locality of *S. guatemalana*.

Solaenogona guatemalana Hoffman
Figures 173–176

Solaenogona guatemalana Hoffman, 1950, J. Washington Acad. Sci., 40: 91–92, figs. 1, 2, 4, ♂; 3, ♀.

Types. Male holotype, female paratype, and many other specimens from between Santa Cruz del Quiché and Totonicapán ("Santa Cruz Quiche" and "Totonicapam" in original description), collected 16 May 1906 by O. F. Cook, deposited in USNM (No. 1883), examined.

Diagnosis. Distinct from S. *chiapas*, the only other known species, as indicated in the above key.

Description of male holotype. Length, 22.5 mm, A3 = 1.15 mm. Ocelli 28 on both sides, in 7 regular series. Pigmentation as usual in *Cleidogona*, olive-brown with segmental muscle scars pale brown to white. Anterior gonopods: sternum produced into notched extension between coxae; colpocoxites massive, well sclerotized (Fig. 173), in anterior view with a depression in frontal area, lateral emargination poorly developed; subapical and apical spines both narrow and acuminate. In lateral view (Fig. 174), posterior process of colpocoxite massive, rounded, narrowest near attachment to colpocoxite, distally cupped and fringed. Telopodites small, pointed, abruptly angular, basally fused. Posterior gonopods (Fig. 175): coxa with vestigial gland opening prominent near base, second and third segments subequal, second segment slightly clavate; distal three segments fused, indistinct, claw present. Legs 10: coxae elongate, sinuous, depressed, bearing glands, lacking knobs or plates. Legs 11: similar to legs 10. Sternum 12: median process bulbous, with small distal hook.

Description of female paratype. Length, 21 mm, A3 = 1.15 mm. Nonsexual characters as in male. Cyphopods (Fig. 176): similar to those of *Cleidogona*, quite distinct from those of species of *Pseudotremia;* valves basally fused, lateral valves the broadest; postgenital plate low, weakly sclerotized, without a median shield.

Distribution. Known only from the type locality.

Solaenogona chiapas n. sp.

Figures 177–180

Types. Male holotype, female paratype, and several other specimens of both sexes from 33.7 mi. north of Huixtla, Chiapas, Mexico, elev. 6000 ft., collected 26 February 1966 by G. Ball and D. Whitehead. The specific name is a noun in apposition and refers to the type locality.

Diagnosis. Distinct from S. *guatemalana* in the characters mentioned in the key, and other details of the gonopods.

Description of male holotype. Length, 23 mm, A3 = 1.17 mm. Ocelli 28 on each side, in 6 series, plus single ocellus. Coloration like that of S. *guatemalana.* Anterior gonopods: sternum subquadrate (Fig. 177), not produced between coxae as in S. *guatemalana;* colpocoxites very elaborate, lateral emargination deep, subtended by curved, transparent plate with serrate margins; subapical spine with 2 branches, anteriormost evenly curved laterad, posteriormost extending posteriad, then sharply ventrad and evenly curved anteriad; apical spine ending in small plate. Posterior process larger, more robust than in S. *guatemalana,* broader at point of attachment. Telopodites small, irregular, basally fused, embracing posterior processes of colpocoxites and fitting into special recesses on posterior processes (Fig. 178). Posterior gonopods: suture between coxa and second segment indistinct (Fig. 179), 3 apical segments fused, claw absent. Legs 10 and 11: as described for S. *guatemalana.*

Description of female paratype. Length, 23 mm, A3 = 1.15 mm. Nonsexual characters as in male. Cyphopods: valves distinctly overlapping (Fig. 180); postgenital plate with large, heavily sclerotized median shield.

Distribution. Known only from type locality.

Genus *Cleidogona* Cook

Cryptotrichus Packard, 1883, Proc. Amer. Philos. Soc., 21: 189; preoccupied by *Cryptotrichus* Schaufuss 1865 (Coleoptera).

Campodes, Bollman, 1893, U. S. Nat. Mus. Bull., 46: 120. Not *Campodes* C. L. Koch.

Cleidogona Cook, 1895, *in* Cook and Collins, 1895, J. New York Acad. Sci., 9: 3; new name to replace *Cryptotrichus* Packard. Cook and Collins, 1895, Ann. New York Acad. Sci., 9: 41; Hoffman, 1950, J. Washington Acad. Sci., 40: 88–89 (key and list of species); Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull., 212: 89–92 (list of species); Loomis, 1968, U. S. Nat. Mus. Bull., 266: 66–68 (list of species).

Mexiceuma Verhoeff, 1926, Zool. Anz., 68: 112; Hoffman, 1950, J. Washington Acad. Sci., 40: 90 (key and list of species); Loomis, 1968, U. S. Nat. Mus. Bull., 266: 68 (list of species). NEW SUBJECTIVE SYNONYMY.

Rhabdarona Chamberlin and Mulaik, 1941, J. New York Entomol. Soc., 49: 60; Hoffman, 1950, J. Washington Acad. Sci., 40: 91 (key and list of species); Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull., 212: 96 (list of species). NEW SUBJECTIVE SYNONYMY.

Cavota Chamberlin, 1942, Bull. Univ. Utah, 33: 8; Hoffman, 1950, J. Washington Acad. Sci., 40: 89 (key and list of species); Loomis, 1968, U. S. Nat. Mus. Bull., 266: 66 (list of species). NEW SUBJECTIVE SYNONYMY.

Hirsutogona Kraus, 1954, Senck. Biol., 35: 329; Loomis, 1968, U. S. Nat. Mus. Bull., 266: 68 (list of species). NEW SUBJECTIVE SYNONYMY.

Mecistopus Loomis, 1959, J. Washington Acad. Sci., 49: 162. NEW SUBJECTIVE SYNONYMY.

Acakandra Loomis, 1964, Fieldiana, 47: 99; 1968, U. S. Nat. Mus. Bull., 266: 66 (list of species). NEW SUBJECTIVE SYNONYMY.

Costaricia Loomis, 1966, Proc. Biol. Soc. Washington, 79: 226; 1968, U. S. Nat. Mus. Bull., 266: 66 (list of species). NEW SUBJECTIVE SYNONYMY.

Type species. Of *Cleidogona*, *Spirostrephon caesioannulatus* Wood, by original designation; of *Mexiceuma*, *M. maculata* Verhoeff, by monotypy; of *Rhabdarona*, *R. bacillipus* Chamberlin and Mulaik, by monotypy; of *Cavota*, *C. crucis* Chamberlin, by monotypy; of *Hirsutogona*, *H. minutissima* Kraus, by original designation; of *Mecistopus*, *M. varicornis* Loomis (= *Cleidogona bacillipus* Chamberlin and Mulaik), by monotypy; of *Costaricia*, *C. curvipes* Loomis, by monotypy; *of Acakandra*, *A. austrina* Loomis, by monotypy.

Loomis (1966) correctly interpreted the proposal of the generic name *Cleidogona*. Cook proposed the name in an introductory note to the revision of the North American Craspedosomatidae published by Cook and Collins (1895). In a footnote, Cook clearly states that the name is to replace the preoccupied *Cryptotrichus* Packard; as the type species of *Cryptotrichus* was *Spirostrephon caesioannulatus* Wood, *caesioannulatus* must be the type species of *Cleidogona* as well. Most later authors have followed Cook and Collins (1895) in considering *C. major* the type of *Cleidogona*, a proposal they (Cook and Collins) made with the expectation that *C. major* would eventually fall as a synonym of *C. caesioannulata*, a peculiar idea, since they had the correct concept of *caesioannulata* to begin with. The gender of the name *Cleidogona* is feminine; the meaning is obscure.

Notes on synonymy. The genus *Mexiceuma* was erected by Verhoeff on *M. maculata* in 1926, and was made the type genus of the family Mexiceumidae. This is yet another example of Verhoeff's astonishing tendency to publish a bewildering series of names without examining related material. *Mexiceuma maculata* is a perfectly typical species of *Cleidogona*, and in fact has been described under new names in that genus twice since Verhoeff's original account. *Rhabdarona bacillipus*, type species of *Rhabdarona*, and *Mecistopus varicornus*, type species of *Mecistopus*, are synonyms. The species is a typical *Cleidogona*, northernmost representative of the Mexican group centering around *C. maculata*. Both genera were based primarily on characters of the posterior gonopods now known to be common to many species of *Cleidogona*. Likewise, *Cavota*, with its single species *C. crucis*, was set up because Chamberlin (1942) considered the presence of an extra segment in the posterior gonopods a generic character; it is not. *Hirsutogona* cannot be differentiated from *Cleidogona* on the characters given by Kraus (1954); the species listed by Kraus as belonging here are members of several different species groups of *Cleidogona*, and the type species, *H. minutissima*, has some of the characters of *Dybasia*. *Costaricia* was diagnosed by the cleft tip of the twelfth sternal process; this is not a generic character, and is found in other *Cleidogona* species. Unfortunately, the unique male holotype of *Acakandra austrina* had no gonopods with it, but the great similarity between that species and *Cleidogona atoyaca* of the species group near *C. minutissima* precludes recognizing the genus as distinct.

Diagnosis. Distinct from *Pseudotremia* and *Solaenogona* in lacking a colpocoxite branch bearing a gland channel; from *Dybasia* in having the sternite of the anterior gonopods completely fused to the coxae; and from *Tiganogona* in the greater complexity of the anterior gonopods and lesser complexity of the posterior gonopod coxae.

Description. Thirty segments. Mentum divided (Fig. 181). Antennae long, article 3 the longest. Ocelli always present, infrequently reduced in number and pigmentation. Body fusiform, widest in males at segment 7, tapering evenly posteriad. Majority of species with nearly cylindrical body segments (Fig. 382), segmental setae on very low tubercles, but some species with 2 outer segmental setae on prominent tubercles (Fig. 274) resembling *Conotyla* (Conotylidae). Surface of segments always smooth, dorsum evenly rounded. Segmental setae small to quite prominent, never spatulate, even in troglobitic species. Sides of segments without prominent lateral striations. Pregonopodal legs of males: legs 1 and 2 slender, 6-segmented, genital openings on second coxae not prominent. Legs 3 through 7 (Fig. 182) strongly crassate, prefemora and femora enlarged and strongly curved mesad. Coxae of legs 7 usually with prominent posterior knobs. Anterior gonopods: highly modified (Figs. 184, 185). Sternum fused to base of coxae, usually extending between colpocoxites for half their length as weakly sclerotized, depressed area. Strong lateral suture from spiracle setting off lateral sternal sclerites. Coxae small, irregular, not fused to one another, extending about half the length of colpocoxites laterally, drawn out anteriorly into prominent knob at juncture of sternum and colpocoxites, usually with lateral patch of setae. Colpocoxites large, variously complex, or simple and falcate, with at least part of posterior margin finely laciniate, fused narrowly to each other in proximal midline. Telopodites sometimes nearly absent, reduced to small knobs at posterior base of coxae, but usually at least one-third length of colpocoxites, sometimes fused basally, but muscularized and movable, simple in shape, usually clavate or spatulate. Posterior gonopods: sternum weak, bandlike. Coxae enlarged, variously lobed; telopodites reduced, 5- to 2-segmented, claw always present. Tenth and eleventh legs with coxae much elongate, sigmoid, bearing coxal glands. Tenth coxae (Fig. 304) sometimes with prominent coxal knob distal to gland opening; eleventh coxae (Fig. 313) usually with sclerotized shelf distal and posterior to gland opening. Twelfth sternite (Fig. 314) usually with anterior peg extending between coxae of tenth and eleventh legs, of various forms. Twelfth coxae somewhat enlarged. Female cyphopods: valves subglobular, but frequently with serrate laminae posteriorly (Fig. 216), moderately setose. Postgenital plate (Fig. 186) usually present, of various forms.

Distribution (See Maps 10, 11). Highlands of Panama, Costa Rica, El Salvador, Honduras, Guatemala; Chiapas Plateau in Mexico north through Central Highlands to southern San Luis Potosí, and in Sierra Madre Oriental to Sierra de el Abra in Tamaulipas (troglobitic species); coastal Oaxaca, Veracruz, Volcán de Colima in Jalisco; from northern Nuevo León to Big Bend region in Texas; North American coastal plain from Mississippi to central Florida north to Virginia, Appalachian Mts. from west central Pennsylvania to Alabama; interior foothills and plains west to Illinois, Missouri, and Arkansas.

Gonopod Anatomy of *Cleidogona*

The gonopods of *Cleidogona major* are typical of those species of *Cleidogona* in which the telopodites are large and movable. The description below is based on material cleared in trypsin.

In an anterior view (Fig. 184), the thin, bandlike portion of the sternum (S) is readily apparent. The arms that extend laterad of the origin of the tracheal apodemes (*TA*) are slightly forked, and fused to the lateral sternal sclerites (S) by an immovable, or only slightly movable, joint. The gonopod coxae (*C*) articulate with the lateral sternal sclerites by means of a basal coxal bar (*CB*). The membranous front plate (*FP*) of the sternum is also attached to the coxae, strongly so near the anterior coxal knobs (*CK*). In uncleared preparations, a large deltoid muscle inserts on the inner surface of this knob, originating on the tracheal apodeme of the opposite side. The colpocoxites (*CC*) are not movable at their joint with the coxae. They are contiguous in the midline and in uncleared preparations often give the impression of being fused there. In posterior view (Fig. 185), it can be seen that the sternum is incomplete posteriorly, the two lateral sternal sclerites (*LSS*) being connected by a membrane. Two posterior coxal arms (*CA*) meet in the midline. The telopodites (*T*) are basally fused, and are inserted through a membrane connecting the mesal faces of the coxae with the posterior faces of the colpocoxites (*CC*). The proximal portions of the tolopodites turn sharply distad, and receive strong muscles both from the tracheal apodemes (*TA*) and coxae. They are freely movable in cleared preparations. The colpocoxites (*CC*) have a subapical laciniate lobe, on which, in freshly killed animals, masses of sperm are sometimes entangled.

There are many additional modifications in other species, but the same basic plan is followed throughout the genus *Cleidogona*, the coxae being particularly similar from species to species. As already seen, in some members of the *major*-group, the apical part of the coxa is drawn out into a process situated about halfway in the length of the colpocoxite. In members of the *caesioannulata*-group (*Cleidogona caesioannulata*, Fig. 380) this process forms a fairly large plate. In members of the genus *Solaenogona* (*Solaenogona chiapas*, Fig. 178) the coxal process is enormous, and is the largest part of the anterior gonopods. In *Cleidogona celerita* (Fig. 374) the colpocoxites are very much expanded posteriorly. In *C. fustis* (Fig. 398) they are reflexed anteriad and deeply notched. In many Mexican species (*C. baroqua*, Fig. 197) they are extremely complex, with numerous spines and knobs. The telopodites vary greatly in size, from almost equal to the colpocoxites (*C. fustis*, Fig. 398), to practically absent (*C. stolli*, Fig. 276). There is no trace of the telopodites in *C. atoyaca* (Fig. 282). In the peculiar *C. forficula* (Figs. 190, 191) the telopodites are as large as the colpocoxites and are wrapped around them.

Cyphopod Anatomy of *Cleidogona*

The cyphopods of members of the genus *Cleidogona* differ in a number of ways from those of *Pseudotremia* species. In *Cleidogona major*, most of the typical features are well developed. In Figure 186, the cyphopod complex and associated leg coxae are seen in posterior view. The coxae of the second legs (*C*) extend lateral to the cyphopods. The coxae of the third legs are not strongly modified, but are slightly excavate to receive the cyphopod valves when they are not extended. As in *Pseudotremia hobbsi*, each cyphopod is composed of four main parts, seen to greater advantage in Figure 183, a ventral view of a single cyphopod. The lateral and mesal valves (*LV, MV*) are fused posteriorly, and the mesal valve is the largest (compare Fig. 186). The seminal receptacle, seen between the valves in Figure 186, consists of a group of teardrop-shaped sacs. The receptacle (*R*, Fig. 183) is much smaller than in *P. hobbsi*. The oviduct pore (*O*) is surrounded by two pairs of postreceptacular bars (*PB*). Unique to many species of *Cleidogona* is the postgenital plate (*PP*, Fig. 186), bearing ventral extensions of various shapes. This structure probably develops from the posterior parts of the second leg coxae, and is extremely useful in taxonomy.

Other Taxonomic Characters

The modifications of coxae 10 and 11 and sternum 12 of males are often of value. Size, as in *Pseudotremia*, is best estimated by the length of the third antennal article (see Diag. 6).

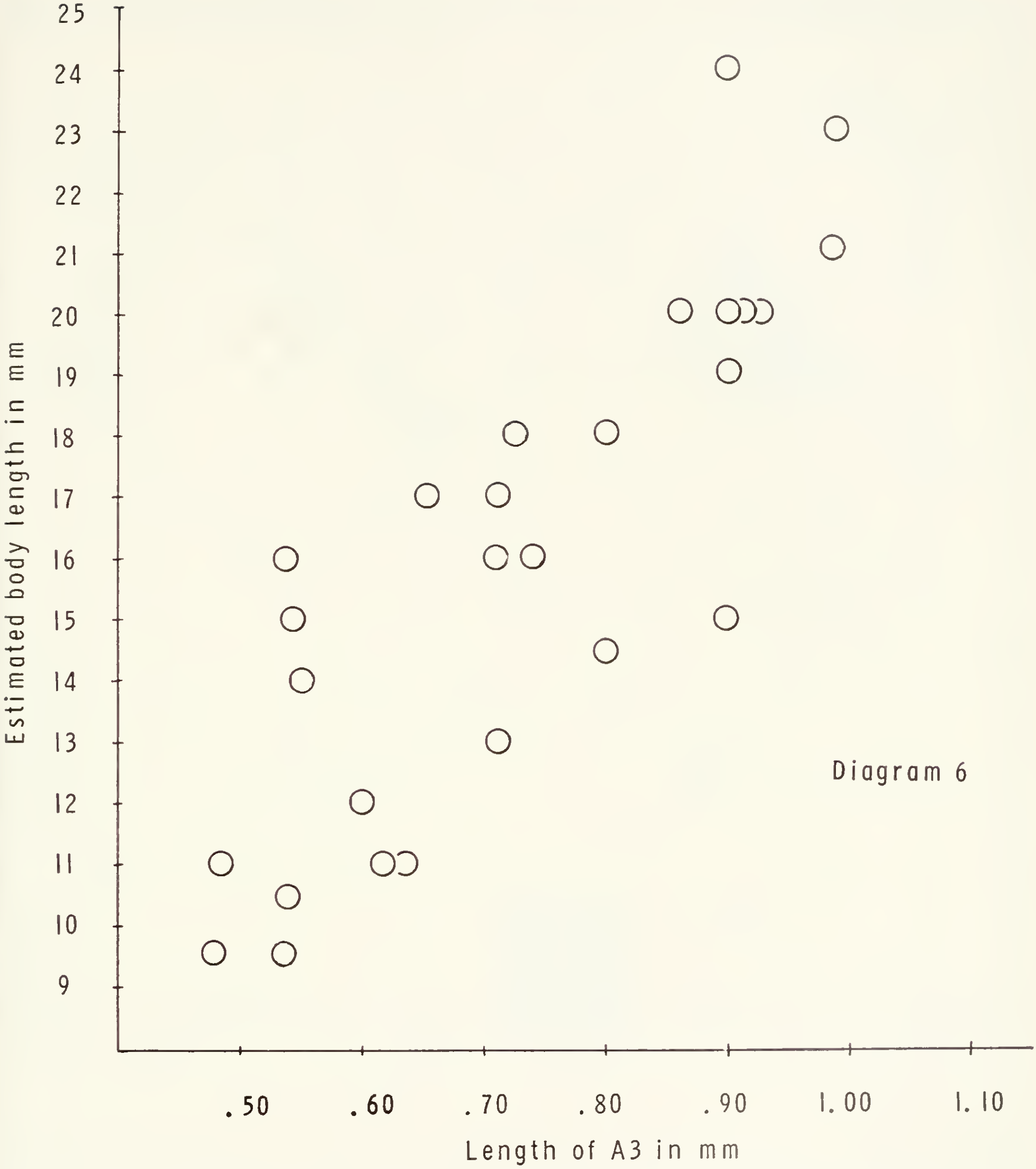
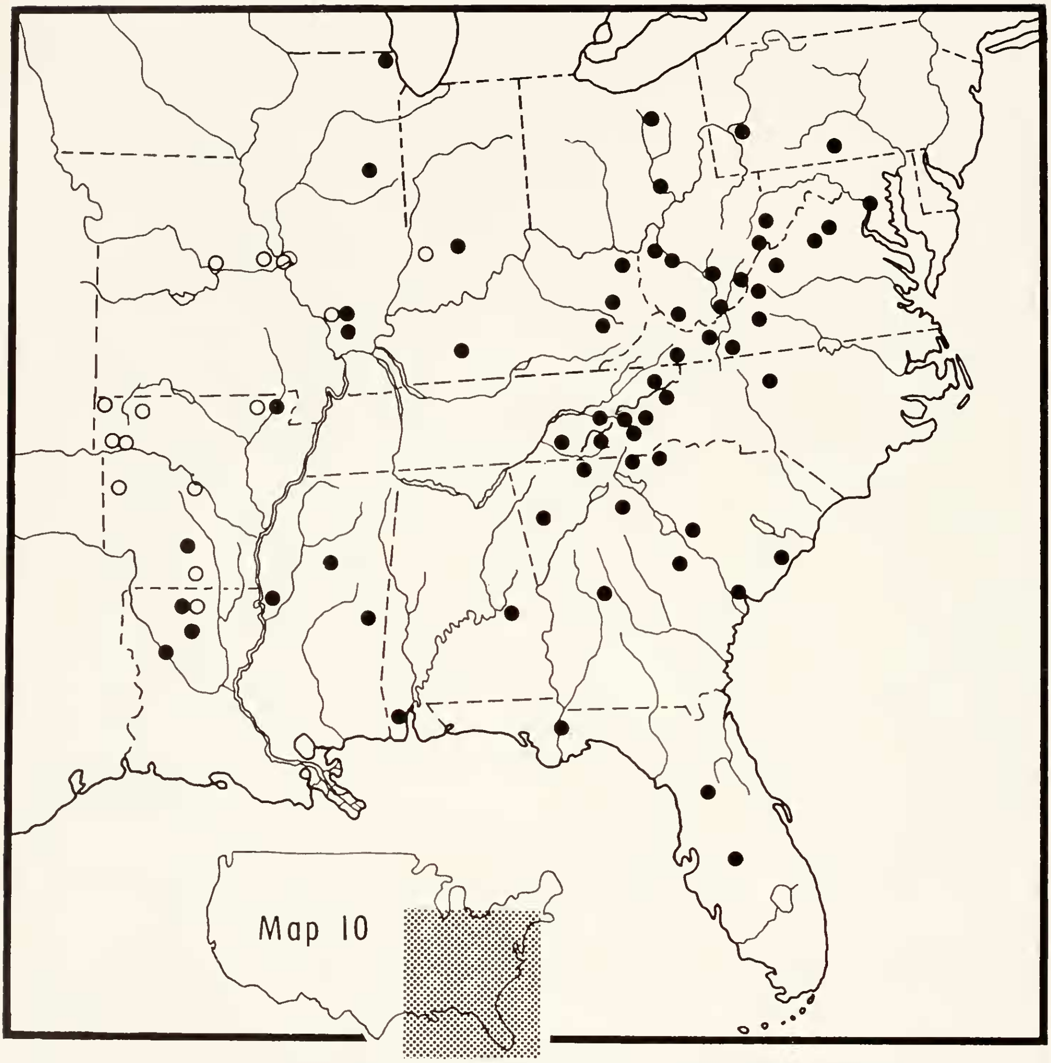


Diagram 6. Graph showing relationship between estimated body length and length of antennal segment three (A3) in holotypes of 27 species of *Cleidogona.*

Evolution, Zoogeography and Species Groups in *Cleidogona*

The evolution of the genus *Cleidogona* is much more difficult to deal with than it is in the genus *Pseudotremia;* there are many more species of *Cleidogona,* and the range of the genus is enormously larger. There are also a few species that seem more or less unrelated to the genus as a whole, and which, applying past standards,

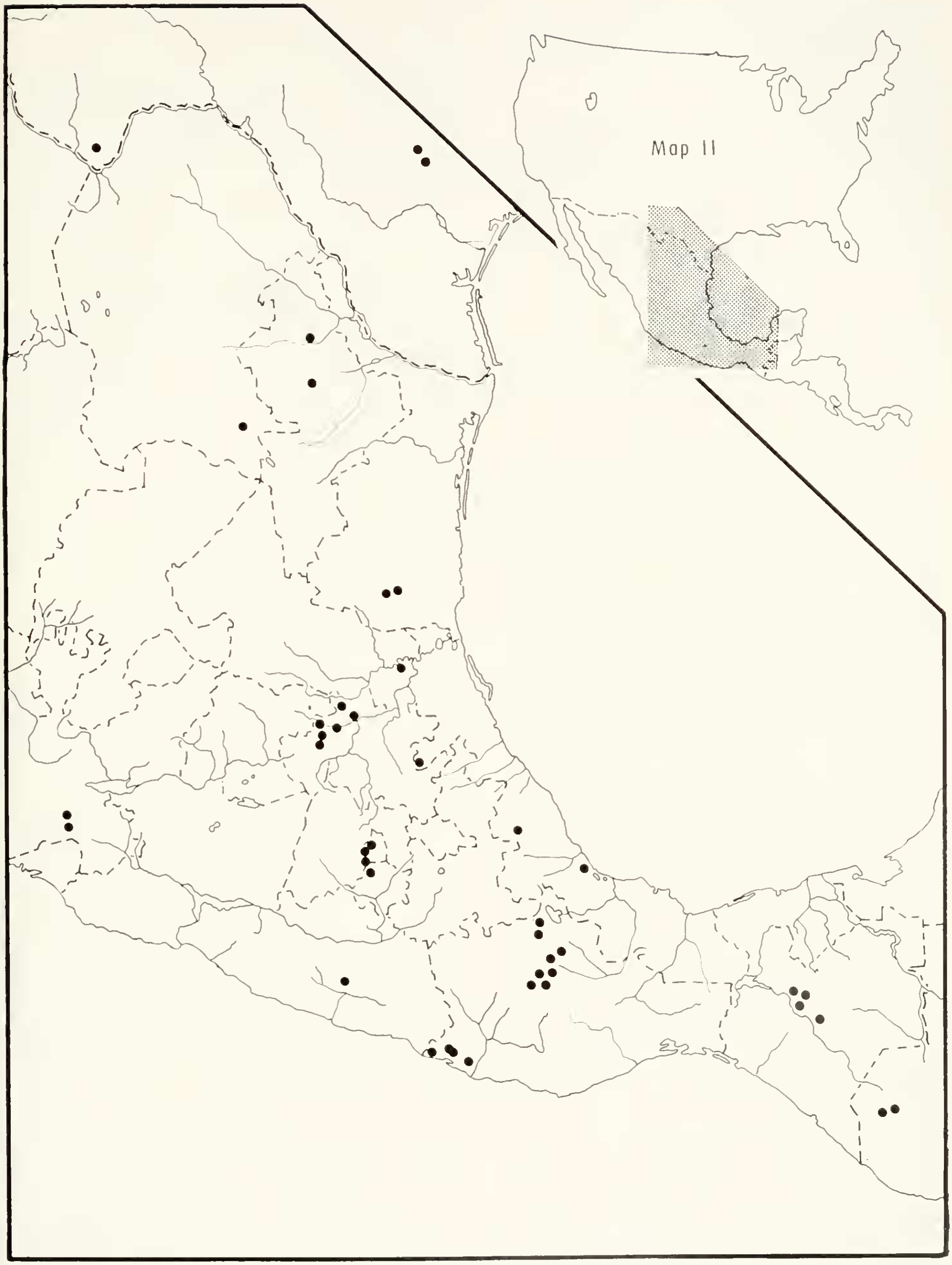


Map 10. Eastern United States, showing distribution of species of *Cleidogona* (dots) and *Tiganogona* (circles).

might even be considered as representing separate genera. In view of these difficulties, the following discussion is presented piecemeal, each species group being taken up in turn, under the larger geographical headings of Mexican and North American species. The species groups are not well defined; they consist of species that appear to be related through gonopod anatomy and geographical distribution, but I think they are more natural than the species groups of *Pseudotremia*.

The Mexican Species

Having already indicated in the discussion of the evolution and zoogeography of the family Cleidogonidae given above that I believe the genus *Cleidogona* to have originated in the southern Mexican highlands, it seems most appropriate to



Map 11. Central Mexico and western Guatemala, showing distribution of *Cleidogona* species (dots). The genus also occurs in Honduras, El Salvador, Costa Rica, and Panama.

begin the discussion of *Cleidogona* with the Mexican species groups that appear to be most primitive, *i.e.*, most like *Solaenogona* and *Pseudotremia.*

Ceibana Group. This group contains the single species, *C. ceibana*, unique in many ways. In an anterior view of the gonopods (Fig. 188), a groove can be seen that recalls the gland channel of *Solaenogona,* and the colpocoxites as a whole are complex. The telopodites apparently curve around the colpocoxites, but they are broken off in the unique type. Until more species are discovered in this group, its relationship to the rest of the genus is obscure.

Crucis Group. As in *Solaenogona,* the colpocoxites are extremely complex but, unlike that genus, the telopodites of this group are large and movable. The distribution of the group, with many distinct species in the highlands of Oaxaca and extending northward into Veracruz, needs clarification. I think only about half of the species have been described. The posterior gonopods assume a variety of forms and the females have the cyphopod complex more or less elaborate. The evidence of gonopod morphology and distribution indicates that this portion of the genus is most closely related to *Solaenogona,* possibly excepting *C. ceibana.* I believe the complexity of the gonopods is a primitive character, not an advanced one.

Crystallina Group. The two species of this group occur in caves in the Sierra de el Abra region of Tamaulipas and are intermediate in gonopod structure between the *crucis*-group and the *maculata*-group. The colpocoxites are somewhat simplified, and the telopodites are still large and movable. The occurrence of this group in caves, with some troglobitic modifications, may indicate that the *maculata*-group (see below) differentiated in the Pleistocene, since climatic events of that epoch are generally believed responsible for cave relict populations (Mitchell, 1969). I believe the group to be derived from the *crucis*-group, and possibly ancestral to the *maculata*-group.

Maculata Group. In this large group, the colpocoxites are simple, bladelike, and have a nearly right-angled bend in the apical third. The telopodites are of moderate size or reduced, and are usually movable. The group occurs with the greatest variety of species in the Mexican Central Highlands, in the states of Querétaro and the Mexican Federal District, extending northward into Coahuila, San Luis Potosí and into south Texas in the United States. The great number of species and the extension of the range northward indicate that this is a progressive, rapidly speciating group of recent origin. The *maculata*-group is related to the more primitive *crucis*-group through the intermediate *crystallina*-group.

The evidence from gonopod morphology and distribution shows that the North American members of the genus (and likewise the species of *Tiganogona*) are probably descended from a stock near the dividing point between the *crystallina*- and *maculata*-groups (Diag. 7). The present hiatus in the distribution of the genus in the Great Plains may point to a pre-Pliocene date for this movement into North America.

Godmani Group. The *godmani*-group, occurring in Oaxaca and Veracruz, with one species in Querétaro, is a minor offshoot from the *crucis*-group. There are some resemblances to species of the *maculata*-group, but these may be due to convergence. Species of the *godmani*-group are smaller, and the gonopods lack the right-angled bend found in those of the species of the *maculata*-group.

Forficula Group. The very peculiar *C. forficula* may be a development from the *godmani*-group. The gonopods are unique in the Cleidogonidae (Figs. 190, 191).

Rafaela Group. This group represents a parallel development with the *maculata*-group, arising from the *crucis*-group. The gonopod colpocoxites are simple, but very

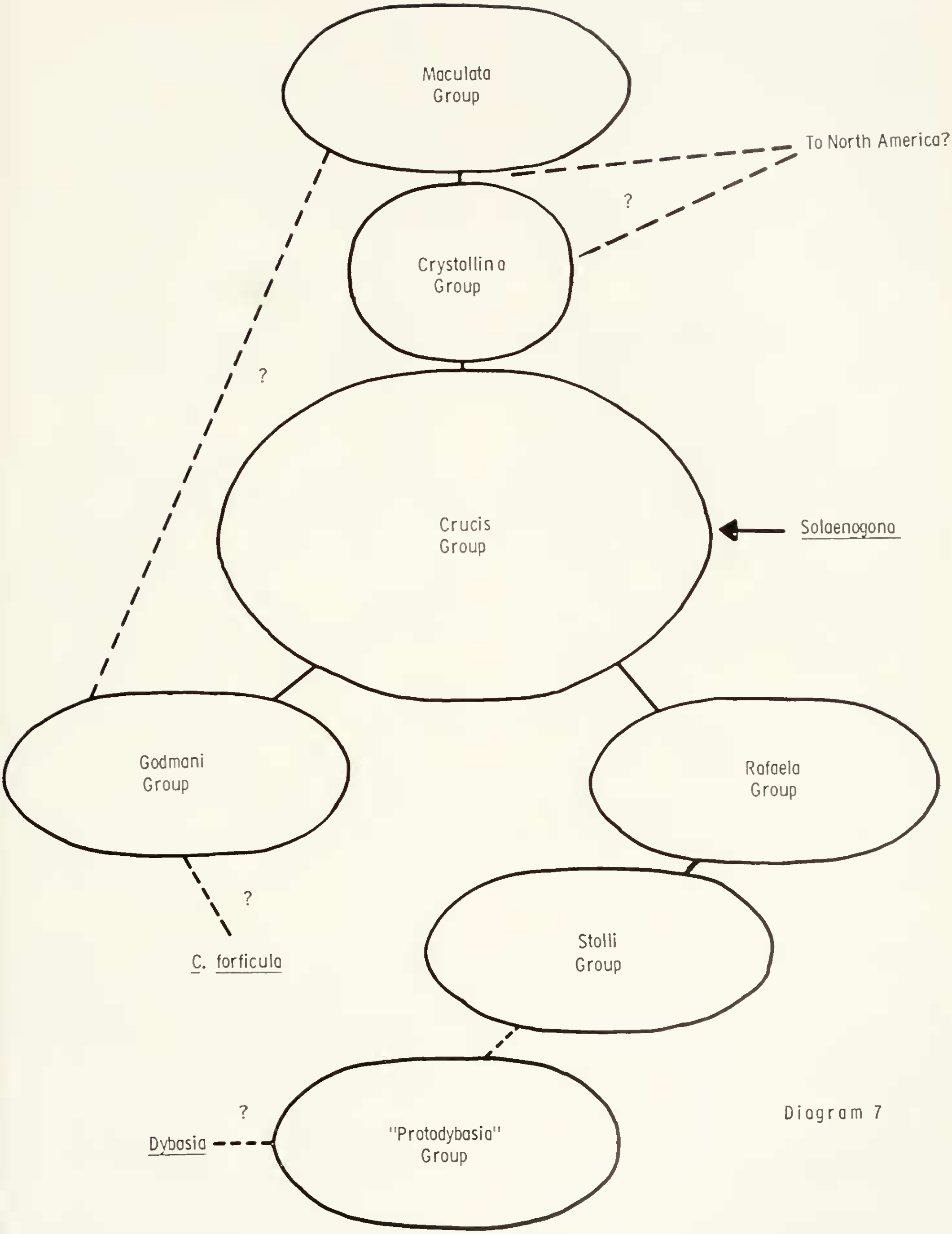


Diagram 7. Possible relationships between species groups of Mexican and Central American *Cleidogona* and *Dybasia*. Lines do not imply direction of evolution unless tipped with an arrowhead. Species groups arranged roughly as they are distributed geographically.

broad in lateral view, and are not bent at a right angle. The telopodites are moderate to small in size. The group as a whole is distributed to the south of the *crucis*-group, in Chiapas and Oaxaca. While the development of the *maculata*-group line has led to the North American species, it seems likely that the *rafaela* line of development has spread southward along the mountain spine of Central America and has given rise to the genus *Dybasia* at its southernmost extension (Diag. 7).

Stolli Group; Proto-Dybasia Group. Both of these groups occur in Chiapas and Guatemala, and represent offshoots from the *rafaela*-group that are intermediate between *Cleidogona* and *Dybasia*. The small, simple colpocoxites, greatly reduced telopodites, and, in the Proto-*dybasia*-group, the sternal processes, all indicate a relationship with *Dybasia* species of Panama, the southernmost representatives of the family.

Summary of discussion of Mexican species. Diagram 7 graphically summarizes the relationships of the various groups of Mexican species. The ovals representing species groups are roughly positioned in the geographical relationship that exists in nature. The *crucis*-group is central to the scheme and is considered the most primitive because of its similarity to the species of *Solaenogona*. Historically, all that can now be said with some assurance is that the genus *Cleidogona* originated from *Solaenogona*-like ancestors and distributed northward through the highlands and mountain ranges of Chiapas, Oaxaca, and Veracruz, gradually differentiating into the *maculata* line in the north, and progressing more slowly southward to differentiate eventually into *Dybasia*. This process has doubtless taken a very long period of time, with many intervening periods of rapid speciation and expansion and of extinction and contraction, these latter resulting in enigmatic single-species remnants like *C. ceibana* and *C. forficula*.

The North American Species

The North American species of *Cleidogona* are probably derived from a Mexican stock close to the present *crystallina*- and *maculata*-groups. The evidence for this is indirect, but there are a few species in Mexico that somewhat resemble species of the *major*-group in North America. With the exception of *C. chisosi*, the North American species form a compact series difficult to separate into species groups.

Chisosi Group. This group contains the single species, *C. chisosi*. It appears to be quite unrelated to any other species of *Cleidogona*, and may later require a separate generic name.

Major Group. This is a very large group of species that has its center of diversity in the south-central Appalachians. The apex of the colpocoxite is divided, and the anterior division may be shieldlike. The coxae bear a posterior projection. The telopodites are large and movable, but not distally clasplike. I consider this group to be derived from Mexican ancestors closely related to the *crystallina*-group, that is, branching off the main line of *Cleidogona* before the trend toward simplification of the gonopods had gone as far as in the species of the *maculata*-group. There has obviously been a great deal of speciation in the Appalachians in the *major*-group, much of it perhaps as recently as the Pleistocene, producing a very close-knit group of similar species. A similar situation exists in several other milliped genera (Hoffman, 1969a). With the possible exception of the species assigned in this study to the genus *Tiganogona*, all of the other North American species groups of *Cleidogona* are satellites of the *major*-group.

Caesioannulata Group. The distribution of the species of this group overlaps with that of species of the *major*-group in western Virginia and North Carolina, and extends westward to Illinois and north to Pennsylvania. The divided tip of the colpocoxite is bent sharply at a right angle, and the coxal projection is large, subquadrate,

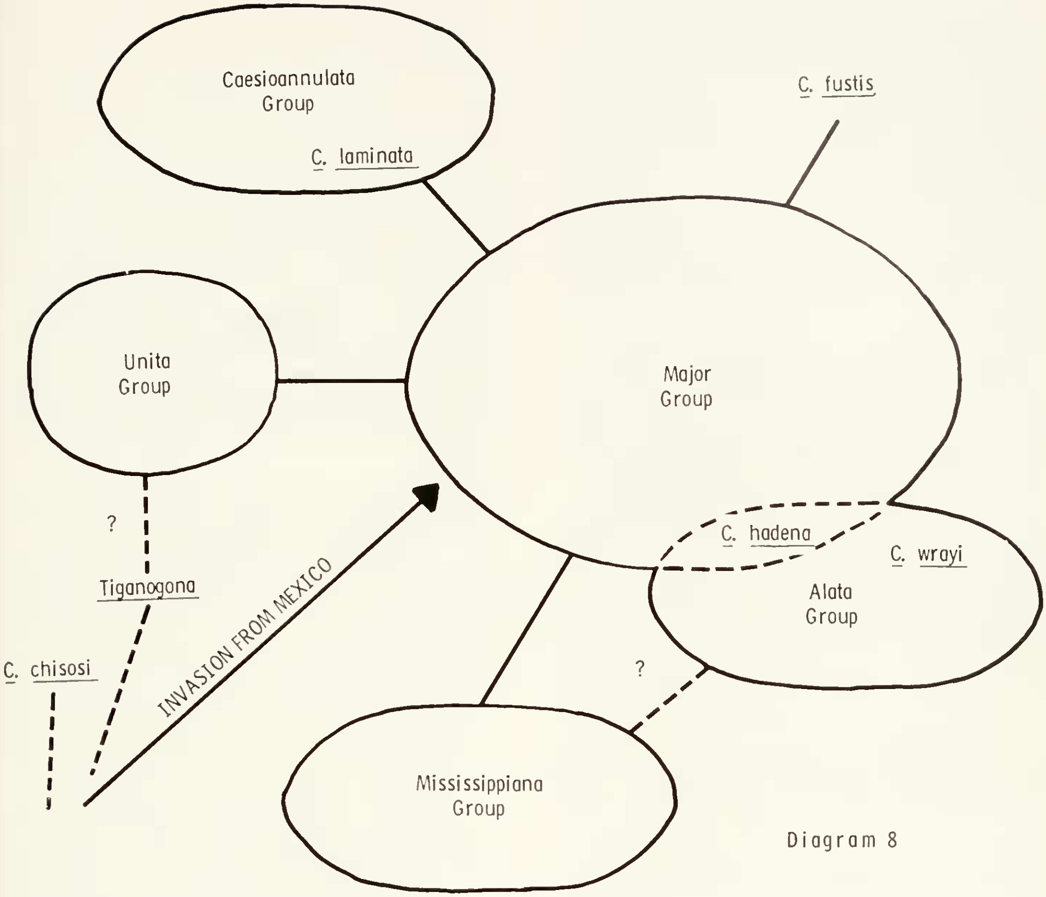


Diagram 8. Possible relationships between species groups of North American *Cleidogona* and *Tiganogana*. Lines do no imply direction of evolution unless tipped with an arrowhead. Species groups are arranged roughly as they are distribute geographically; compare Map 10.

or much inflated (*C. celerita*). The telopodites are clublike or very small. There has been a great deal of confusion about species names in the *caesioannulata*-group.

Unita Group. This small group of two species is a western and southern extension of the *major*-group. The gonopods and the animals themselves are smaller, more simplified, and the colpocoxites are fused at their bases. Too little is known about the distribution of the group to make any confident statements about its origin, except that it definitely is a derivative of the *major*-group and may possibly be related to the species of *Tiganogona.*

Mississippiana Group; Alata Group. The majority of species in these two groups occurs on the Gulf Coastal Plain, Atlantic Coastal Plain, and south into peninsular Florida. They are highly specialized derivatives of the *major* stock; species of the *alata*-group form a series difficult to separate from those of the *major*-group, but the species most similar to *C. major, C. hadena,* occurs in Florida. The gonopod colpocoxites of both groups are thinner, more rodlike, than those of species of the *major*-group. In the *mississippiana*-group, composed of three or four very closely related species, the anterior branch of the divided colpocoxite tip has become a complex process. The telopodites are large, clasplike, and freely movable. The distribution of species of these groups around the Atlantic and Gulf of Mexico Coastal Plains suggests an invasion from the southern Appalachian centers of the *major*-group.

Fustis Group. Cleidogona fustis is a peculiar but apparently very successful northern and western derivative of the *major*-group that has a wide distribution. It has been reported from Indiana and Ohio, and is common in West Virginia and eastern Virginia. The colpocoxites resemble those of *C. major,* but are smaller and lack the coxal projection. The telopodites are much larger in comparison to the colpocoxites than in any other North American species. Cook and Collins' (1895) lost species *C. forceps* may be related to *C. fustis.*

Summary of discussion of North American species. Diagram 8 summarizes the above information. I believe the North American species to be derived from a Mexican stock near the *crystallina*-group, and to have their main center of speciation in the southern Appalachians. Derivatives of the dominant *major*-group have colonized northward, westward, and southward.

It might be mentioned here that two species at the northern extremity of the range of *Cleidogona, C. major* and *C. caesioannulata,* have very large ranges, and are not, in the northern parts of these ranges, sympatric with any other species. Perhaps these two species became adapted to cooler average climatic conditions during the Pleistocene, and when glaciation removed any possible competitors to the north, rapidly expanded in that direction. There is some evidence that this range extension is still continuing; females and immature specimens belonging to *Cleidogona* have been taken in Connecticut and on Cape Cod, the only records of the family from glaciated territory.

The Mexican and Central American Species of *Cleidogona*

Since only a single species, *C. bacillipus,* occurs both north and south of the Rio Grande, and in view of the large number of species of *Cleidogona* to be discussed, it seems most efficient to divide the following species accounts and keys between the Mexican and Central American species and the species occurring in the United States. *Cleidogona bacillipus* appears in both keys, but is discussed below with its Mexican relatives.

KEY TO MALES OF MEXICAN AND CENTRAL AMERICAN *CLEIDOGONA* SPECIES

Males of *C. mexicana* are not known, and that species is not included in this key; for others not included, see section above on species not included in revision.

1a. Body with definite *Conotyla*-like paranota (Fig. 274) on at least anterior segments 2
1b. Segments without paranota, usually cylindrical, or with outermost setae on low rounded swelling 3
2a. Paranota persisting to around segment 17, posterior segments more or less cylindrical; Chiapas .... *laquinta*
2b. Paranota persisting past segment 17; Chiapas .... *conotyloides*
3a. Process of sternum 12 apically cleft; Honduras .... *ceibana*
3b. Process absent or not apically cleft 4
4a. Anterior gonopods (Figs. 190, 191) with telopodites and colpocoxites nearly equal in size, telopodites curving around colpocoxites; Chiapas .... *forficula*
4b. Gonopods not as above 5
5a. Anterior gonopod colpocoxites with a deep, semicircular lateral cleft armed with sharp teeth (Fig. 205); Oaxaca .... *chontala*
5b. Gonopods not as above 6
6a. Anterior gonopod coxae with acuminate process from posterior part of setose region (Fig. 230); Querétaro .... *tizoc*
6b. Gonopods without such a process 7
7a. Anterior gonopod telopodites very thin, curved nearly in a circle, apically divided (Fig. 242); Hidalgo .... *xolotl*

7b. Anterior gonopod telopodites not as above 8

8a. Posterior gonopod coxae with long mesal spatulate process (Fig. 251); Veracruz ..... *tequila*

8b. Posterior gonopod coxae without such a process 9

9a. Anterior gonopod colpocoxites apically pointed (Fig. 254); Oaxaca ..... *hauatla*

9b. Anterior gonopod colpocoxites not as above 10

10a. Body not pigmented, chalky white or pale gray 11

10b. Body normally pigmented 14

11a. Ten to 15 ocelli, ocelli not pigmented; caves in Veracruz ..... *crucis*

11b. More than 20 ocelli, usually pigmented 12

12a. More than 25 ocelli; gonopods (Figs. 197, 198) elaborate; Sótano de San Augustín, Oaxaca ..... *baroqua*

12b. Less than 22 ocelli (usually 20); gonopods simpler (Figs. 221, 217); caves in Sierra de el Abra region, Tamaulipas 13

13a. Gonopods as in Fig. 217 ..... *crystallina*

13b. Gonopods as in Fig. 221 ..... *pecki*

14a. Anterior gonopod colpocoxites with transparent, small lateral teeth (Figs. 201, 209) 15

14b. Colpocoxites lacking such teeth 17

15a. Anterior gonopod colpocoxites with a subapical retrorse rod (Fig. 202); Oaxaca ..... *gucumatz*

15b. Anterior gonopod colpocoxites lacking such a rod 16

16a. Sternum with triangular anterior processes (Fig. 284); El Salvador ..... *minutissima*

16b. Sternum lacking such processes, gonopods as in Fig. 209; Oaxaca ..... *mixteca*

17a. Anterior gonopod colpocoxites with rugae or corrugations on anterior basal part (Figs. 278, 244, 226) 18

17b. Colpocoxites without such corrugations 22

18a. Corrugations extending all across anterior basal surface of colpocoxite, not limited by heavy lateral or mesal ridge (Fig. 226); region of Mexico City *maculata*

18b. Corrugations limited laterally by a heavy ridge (Figs. 278, 244, 236) 19

19a. Telopodites of anterior gonopods short, decurved (Fig. 278); Chiapas ..... *decurva*

19b. Telopodites long or short, upright, not decurved 20

20a. Body less than 10 mm long; Querétaro ..... *mayapec*

20b. Body more than 16 mm long 21

21a. Gonopods as in Fig. 236; Oaxaca *camazotz*

21b. Gonopods as in Fig. 244; Texas, Coahuila, Nuevo León ..... *bacillipus*

22a. Telopodites of anterior gonopods absent (Fig. 282); Veracruz ..... *atoyaca*

22b. Telopodites present 23

23a. Telopodites very short, decurved (Figs. 276, 286) 24

23b. Telopodites not as above 25

24a. Gonopods as in Fig. 276; Guatemala ..... *stolli*

24b. Gonopods as in Fig. 286; El Salvador ..... *mirabilis*

25a. Anterior gonopod colpocoxites with denticulate subapical process (Figs. 213, 214); Oaxaca ..... *chacmool*

25b. Anterior gonopod colpocoxites without such a process 26

26a. Anterior gonopod colpocoxites in lateral view less than one-fourth as broad as long (Figs. 260, 264) 27

26b. Anterior gonopod colpocoxites in lateral view more than one-sixth as broad as long (Figs. 248, 257) 28

27a. Anterior gonopod colpocoxites with oblique ridge in anterior view (Fig. 263); Mexico City area ..... *rafaela*

27b. Gonopods not as above, oblique ridge absent; Oaxaca ..... *zapoteca*

28a. Colpocoxites of anterior gonopods strongly diverging (Fig. 257); Querétaro ..... *totonaca*

28b. Colpocoxites not strongly diverging 29

29a. Gonopods as in Fig. 248; Guatemala ..... *godmani*

29b. Gonopods as in Figs. 232–233; Hidalgo ..... *zimapaniensis*

Cleidogona mexicana (Humbert and Saussure)
Figure 187

Craspedosoma mexicanum Humbert and Saussure, 1869, Rev. Mag. Zool. (2), 21: 153.

Cleidogona mexicana, Cook and Collins, 1895, Ann. New York Acad. Sci., 9: 52; Loomis, 1968, U. S. Nat. Mus. Bull., 266: 67.

Types. Female holotype from "Eastern Cordillera," Mexico, deposited in Natural History Museum of Geneva, Switzerland, examined.

Diagnosis. In the absence of males, no diagnostic characters can be described.

Description of female holotype. Length, about 20 mm; A3 = 0.90 mm. About 28 ocelli in the usual arrangement. Cyphopods (Fig. 187) simple, valves unmodified; postgenital plate narrowly quadrate, apex irregular.

Notes. In the absence of males and definite locality records, little can be said about this species. The holotype is completely bleached, making some characters (ocelli number, coloration) difficult to observe.

Cleidogona ceibana Chamberlin
Figures 188, 189

Cleidogona ceibana Chamberlin, 1922, Proc. U. S. Nat. Mus., 60: 11, plate 6, figs. 1–6, ♂.
Hirsutogona ceibana, Kraus, 1954, Senck. Biol., 35: 329 (placed in *Hirsutogona* with doubt).

Types. Male holotype from La Ceiba, Honduras, in USNM, Type No. 822, examined.

Diagnosis. Completely distinct in the form of the gonopods from any other species of *Cleidogona;* the posterior fimbriate portion of the anterior gonopod (Fig. 189) is especially diagnostic.

Description of male holotype. Length, about 14 mm, A3 = 0.55 mm. Ocelli 21 on both sides of head, in 5 rows plus single ocellus. Coloration light, but typical, fulvous brown with darker markings around points of muscle attachment. Anterior gonopods: in anterior view (Fig. 188), sternum broad, extending between coxae, deep groove in median portion. Coxae rounded, densely setose; colpocoxites complex apically and with vaguely indicated groove on anterior face lying in depression. In lateral view (Fig. 189) lateral sternal sclerite large; colopocoxite with posterior fimbriate area. Telopodites broken off (?) in type, with a large wing basally, rodlike branch curving lateral of colpocoxites. Posterior gonopods: not found in vial with holotype, described by Chamberlin (1922) as follows: "... first joint is nearly as long as the second; it is thick proximally and bends a little and narrows just distad of the middle . . . process on base small. The second joint is strongly clavate. . . ." Coxa 10 elongate, not knobbed, gland on long petiole. Coxa 11 with sharp, spike-shaped branch above gland. Twelfth sternum with large, apically cleft process.

Female unknown.

Distribution. Known only from the type locality.

Notes. This species resembles species of *Solaenogona* in certain respects and links that genus with *Cleidogona.* Loomis (1966) overlooked the illustrations and description of Chamberlin (1922) when he set up the genus *Costaricia* for *C. curvipes* on the basis of the cleft twelfth sternal process in that species. Kraus (1954) had not seen specimens, and assigned *C. ceibana* to *Hirsutogona* with doubt.

THE *FORFICULA* GROUP

Cleidogona forficula n. sp.
Figures 190–192

Types. Male holotype from San Cristobal de las Casas, Chiapas, Mexico, collected 14–16 July 1950 by C. and M. Goodnight. The specific name, an adjective, refers to pincerlike gonopods.

Diagnosis. The subequal, interlocking telopodites and colpocoxites of this species distinguish it from all other species of *Cleidogona.*

Description of male holotype. Length, 16 mm; antennae missing. Ocelli 24 on left side, 25 on right side, in 4 rows plus single ocellus. Coloration typical. Segmental shoulders moderately developed as rounded knobs around lateralmost seta on each segment. Anterior gonopods: in anterior view (Fig. 190) sternum transverse, extending between coxae; coxae flattened, with few setae. Colpocoxites upright, rodlike; telopodites visible, curving anteriad of colpocoxites about midlength, thin, laminate, edges sinuous. In posterior view (Fig. 191), colpocoxites apically divided, posterior branch densely fimbriate, anterior branch platelike; telopodites in contact basally; coxae extending nearly to midline. Posterior gonopods: coxa with large knob bearing vestigial gland aperture (Fig. 192) otherwise typical. Legs 10 and 11 absent from holotype. Sternal process of twelfth sternum small, subtriangular lamella or ridge.

Female unknown.

Distribution. Known only from the type locality.

Notes. The relationships of this species are very obscure. No other Mexican species of *Cleidogona* even remotely resembles it in gonopod anatomy. If additional species are discovered, a separate generic name may be justified.

THE *CRUCIS* GROUP

The species of this group have elaborate modifications of the apical part of the colpocoxites of the anterior gonopods, and in this way resemble species of *Solaenogona* and *Cleidogona ceibana*. The telopodites are well developed and are distally expanded. The female genitalia are simple, with few elaborations of the valves and a subquadrate or bluntly triangular postgenital plate.

Cleidogona crucis (Chamberlin)
NEW COMBINATION
Figures 193–196

Cavota crucis Chamberlin, 1942, Bull. Univ. Utah, 33: 8, figs. 3–7, ♂.

Types. Male holotype from Cueva de Atoyac, Veracruz, type said to have been deposited in Escuela Nacional, Mexico City (Chamberlin, 1942), not seen. The specific name probably makes reference to the state of Veracruz, "True Cross."

Diagnosis. The only species of the group lacking pigment and having less than 20 ocelli.

Description of male from type locality. Length, 15 mm; A3 = 0.65 mm. Ocelli 10, colorless, irregularly arranged in about 3 rows. Totally without pigment. Body segments cylindrical. Anterior gonopods: in anterior view (Fig. 193), sternum broad; coxae with group of 4–5 setae. Colpocoxites with subterminal lateral branch divided apically into 4 small lobes. In lateral view (Fig. 194), telopodite large, cupped ventrad, posterior division with serrate lamella. Posterior gonopods: coxa rather slender, without conspicuous lobes; otherwise typical (Fig. 195). Coxa 10 elongate, cylindrical, gland on short chitinous petiole. Coxa 11 with acuminate process above gland, thin chitinous piece extending basally behind gland. Sternal process 12 typical, acuminate ventrally, dorsal portion of tip thickened, of moderate length.

Description of female from type locality. Length, 14 mm; A3 = 0.62 mm. Nonsexual characters as described for male. Cyphopods: lateral valves of cyphopods much thicker than median valves in posterior view (Fig. 196); postgenital plate broad, transparent, with vague radiating ridges from thickened midline.

Distribution. In addition to the type locality, also known from: VERACRUZ: Cueva de Ojo de Agua Grande, near Cordoba, 4.5 mi. north of Potrero Viejo and 6 mi. northwest of Paraje Nueva, 3 August 1967, J. Reddell, ♂; 7 August 1969, S. Peck, ♂♂. A large collection of both males and females was taken from the type locality by S. and J. Peck, 6 August 1969.

Notes. Cueva de Atoyac and Cueva de Ojo de Agua Grande are separated by about 10 miles (S. Peck, personal communication). The description given by Chamberlin (1942) differs from the above in a few details; the holotype is said to have 14 ocelli in four rows. The posterior gonopods are shown with six segments. In all males examined by me, a rather weak suture, but not a joint, was visible near the basal part of the posterior gonopod coxae (Fig. 195), and Chamberlin may have mistaken this for an actual articulation. This species is a true troglobite.

Cleidogona baroqua n. sp.
Figures 197–200

Types. Male holotype, female paratype types from Sótano de San Augustín, Hauatla de Jiménez, Oaxaca, collected 28 December 1966 by T. Raines. The species name refers to the elaborate appearance of the anterior gonopods.

Diagnosis. Unlike any other species of the group, the apical part of the anterior gonopod colpocoxites are developed into a curved lamella with a denticulate margin; the animals are depigmented but have normal ocelli.

Description of male holotype. Length, 27 mm, A3 = 1.53 mm. Ocelli, 27 on each side in 6 rows plus single ocellus, regular in size and lightly pigmented. Body lacking pigment. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 197) sternum extending high up between colpocoxites, broad, with 2 slight depressions near midline. Coxae elongate, densely setose; colpocoxites with apical curved lamella with denticulate margin curving around rodlike mesal subapical branch. In lateral view (Fig. 198), colpocoxite lamella narrowed in midlength, at right angle to body of colpocoxite; telopodite short, stout, pressed against rounded chitinous mass occupying center of posterior portion of colpocoxites, with short apical hook. Posterior gonopods: coxa (Fig. 199) with complex basal lobes, including long rodlike lobe nearest base (vestigial gland?); widest part of second segment near middle of length. Remaining segments reduced, typical. Coxae 10 not strongly modified, glands sessile or nearly so. Coxae 11 with prominent chitinous plates above glands. Sternal process 12 as usual, as described for *C. crucis.*

Description of female paratype. Length, 25 mm, A3 = 1.50 mm. Nonsexual characters as described for male. Cyphopods: coxae of legs 2 with prominent rugose knobs posteriorly; valves not ornamented (Fig. 200); postgenital plate low, rounded.

Distribution. Known only from type locality.

Notes. Though the three individuals comprising the type collection lack pigment except around the ocelli, this species may not be a true troglobite. It is the largest Mexican *Cleidogona.*

Cleidogona gucumatz n. sp.

Figures 201–204

Types. Male holotype, female paratype and other specimens from 1.5 mi. northeast of El Punto, on road to Ixtlán de Juarez, Oaxaca, elev. 7500 ft., collected 3 September 1961 by R. M. Bogert. The species name is a noun in apposition, the name of the hero of the Mayan epic, *Popol Vuh.*

Diagnosis. The coxae are low and do not extend laterally along the colpocoxites; the telopodites are rodlike, rather than cupped and apically expanded as in the preceding two species.

Description of male holotype. Length, 17 mm, A3 = 0.80 mm. Ocelli 28, in 7 rows. Coloration typical. Segments cylindrical. Anterior gonopods: colpocoxites and sternum apparently completely fused in anterior view (Fig. 201); colpocoxites with retrorse corrugated rod extending basally from upper anterior part, laterally with series of small, transparent teeth. In lateral view (Fig. 202), telopodite more rodlike than in preceding two species. Coxa with only two setae. Posterior gonopods: typical of genus (Fig. 203), coxa with basal lobe, narrowed near middle; second segment with broadest point below distal end. Coxa 10 elongate, curved, gland with petiole. Coxa 11 with short plate above gland. Process of sternum 12 acuminate-triangular, shorter than in preceding species.

Description of female paratype. Length, 15.5 mm, A3 = 0.80 mm. Nonsexual characters as in male. Cyphopods: lateral valves (Fig. 204) with broad flanges; postgenital plate narrowly triangular.

Distribution. Known only from the type locality.

Cleidogona chontala n. sp.

Figures 205–208

Types. Male holotype and four female paratypes from 27.5 mi. south of Valle Nacional, Oaxaca, elev. 5600 ft., collected 15–16 August 1965 by G. Ball and D. Whitehead. The specific name is an adjective referring to the Chontal Indians of Oaxaca.

Diagnosis. The deep, denticulate cleft on the lateral margins of the anterior gonopods distinguishes this species from any other.

Description of male holotype. Length, 16 mm, A3 = ? (antennae missing from all specimens). Ocelli 27, in 6 rows. Coloration typical. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 205), sternum low, subtriangular between gonopod coxae, coxal knobs prominent, coxae without setae, solidly fused to colpocoxites; with deep lateral excavation with basal margin denticulate, distal margin drawn out into long acuminate process. Colpocoxites bluntly quadrate, posteriorly bladelike, thin posterior portion with tooth visible in lateral view (Fig. 206) near midlength. Telopodites curved, not apically expanded. Posterior gonopods: similar to those of *C. gucumatz,* but with widest part of second segment near midlength, not at apical end (Fig. 207).

Description of female paratype. Length, 16 mm, antennae missing. Nonsexual characters as in male. Cyphopods: (Fig. 208) both lateral and median valves with carinae, postgenital plate broad, transparent.

Distribution. Known only from the type locality.

Cleidogona mixteca n. sp.
Figures 209–212

Types. Male holotype, female paratype and other males and females from 54.1 mi. south of Valle Nacional, Oaxaca, elev. 8300 ft., collected 3 May 1966 by G. Ball and D. Whitehead. The species name, an adjective, refers to the Mixtec culture of pre-Columbian Mexico.

Diagnosis. The apical part of the anterior gonopod colpocoxites is corrugated, rather than smooth, as it is in *C. chontala;* the small, transparent lateral teeth are much more numerous than in *C. gucumatz.*

Description of male holotype. Length, 16 mm, A3 = 0.83 mm. Ocelli 26 in 5 rows. Coloration typical, somewhat darker than usual. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 209), sternum broadly expanded between colpocoxites, lightly depressed; only coxal knobs visible in anterior view; coxae without setae. Colpocoxites with series of lateral transparent teeth, mesoapical region finely corrugated. In lateral view (Fig. 210), apical part of colpocoxite hoodlike, blade portion concealed, with a few weak ridges laterally. Telopodite curved, rodlike. Posterior gonopods: coxa typical (Fig. 211); second joint not as broadly expanded as in preceding 2 species. Coxa 10 elongate. Coxa 11 with a small plate distal to gland. Process of sternum 12 typical.

Description of female paratype. Length, 15.5 mm, A3 = 0.80 mm. Nonsexual characters as in male. Cyphopods (Fig. 212): similar to those of *C. gucumatz,* postgenital plate somewhat narrower.

Distribution. Besides the type locality, the following: OAXACA: 30.2 mi. south of Valle Nacional, 8300 ft. elev., 16 August 1965, G. Ball and D. Whitehead, ♂; 88.5 mi. south of Valle Nacional, 4100 ft. elev., G. Ball and D. Whitehead, ♂♀♀.

Notes. Cleidogona mixteca is clearly related to *C. gucumatz.*

Cleidogona chacmool n. sp.
Figures 213–216

Types. Male holotype, female paratype and another female from 60.6 mi. south of Valle Nacional, Oaxaca, 7500 ft. elev., collected 18 August 1965 by G. Ball and D. Whitehead. The species name is a noun in apposition, and refers to the Aztec death god.

Diagnosis. The subapical branch of the anterior gonopod colpocoxite pointing distad (Fig. 214) is diagnostic.

Description of male holotype. Length, 25 mm, A3 = 1.10 mm. Ocelli 28 in 7 rows. Coloration typical. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 213), sternum and colpocoxites appear fused, sternum not extending far between colpocoxites. Both apical branches of colpocoxite with small teeth; coxae with only 2 setae. In lateral view (Fig. 214), branches of colpocoxite unequal, anterior subapical branch rodlike, posterior branch broad, with posterior bladelike portion obviously finely fimbriate along posterior margin. Telopodite broadly expanded, posterior portion longest, rugose area in cup between prongs. Posterior gonopods (Fig. 215): coxa narrower than in other species of group; second segment broadly and evenly expanded, widest part just distad of midlength. Coxae 10 and 11 are as described for *C. mixteca*. Process of sternum 12 as usual.

Description of female paratype. Length, 23 mm, A3 = 1.08 mm. Nonsexual characters as described for male. Cyphopods (Fig. 216): similar to those of two preceding species, but knobs of coxae 2 somewhat larger, lateral carinae of lateral valves corrugated.

Distribution. In addition to the type locality, the following: OAXACA: Llano de las Flores, Sierra Juarez, 9300 ft. elev., 17 September 1961, M. R. Bogert, ♂ ♀.

THE *CRYSTALLINA* GROUP

Members of this group have gonopods simpler than those of the preceding group, but the colpocoxites are not bent at a right angle as in the *maculata*-group. They occur in caves in the Sierra de el Abra of southern Tamaulipas, but do not appear to be genuine troglobites.

Cleidogona crystallina n. sp.
Figures 217–220

Types. Male holotype, female paratype and many other specimens from Cueva Chica de la Perra, 6 mi. northwest of Gómez Farias, Tamaulipas, elev. 7000 ft., collected 2 July 1969 by S. Peck and R. Norton. The species name refers to this species' occurrence in nearby Crystal Cave.

Diagnosis. Distinct from the related *C. pecki* in the less acutely angled colpocoxites of the anterior gonopods and the form of the telopodites (Fig. 218). The basal segment of the posterior gonopods (Fig. 219) has a definite articulation about one-third its length from the basal end. The female cyphopods lack the high posterior carinae on the valves found in *C. pecki*.

Description of male holotype. Length, 15 mm, A3 = 0.90 mm. Ocelli 21, somewhat irregular in arrangement, not pigmented. Body not pigmented, or dirty gray in color, blotched darker. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 217), basal part of sternum subquadrate, extending narrowly between colpocoxites; coxae large, setose. Colpocoxites with 2 rounded ridges on anterior side, with lateral projection and subterminal process. In lateral view (Fig. 218), lateral projection with 2 teeth, colpocoxite bent at obtuse angle, bladelike posterior part deeply laciniate. Telopodite with median winglike process. Posterior gonopods (Fig. 219) 6-segmented; second (third?) segment not much broadened. Coxae 10 and 11 as usual; process of sternum 12 of moderate size.

Description of female paratype. Length, 15 mm, A3 = 0.92 mm. Nonsexual characters as in male. Cyphopods (Fig. 220): lateral valves with moderate lateral carinae; postgenital plate much reduced, possibly absent.

Distribution. In addition to the type locality, the following: TAMAULIPAS: Crystal Cave, Rancho de Cielo, near Gómez Farias, no date or collector, ♂; Salamander Cave, 6 mi. northwest of Gómez Farias, 4 July 1969, S. and J. Peck, ♂; Cueva Capilla de la Perra, 8 mi. northwest of Gómez Farias, 2 July 1969, S. Peck and R. Norton, ♂ ♂ ♀ ♀.

Notes. This species may be a troglophile; it has not been collected on the surface. However, the animals are not completely depigmented and have a nearly normal number of ocelli.

Cleidogona pecki n. sp.

Figures 221–225

Types. Male holotype, female paratype and many other specimens from Cueva de la Mina, 6 mi. northwest of Gómez Farias, Tamaulipas, elev. 5000 ft., collected 1 July 1969 by S. and J. Peck. The name honors my friend, Dr. Stewart B. Peck, who collected the type series, and helped in this study in many other ways.

Diagnosis. Closely related to *C. crystallina,* but distinct in the characters given in the diagnosis of that species.

Description of male holotype. Length, 21 mm, A3 = 1.08 mm. Twenty ocelli in about 5 rows, darkly pigmented in some specimens, not pigmented in others. Body not pigmented, chalk white, or slate gray blotched darker (possibly artifact of preservation). Segments cylindrical. Anterior gonopods: in anterior view (Fig. 221), similar in general form to those of *C. crystallina,* but larger, lacking lateral projection and subterminal process; tip of colpocoxites with small cleft. In lateral view (Fig. 222), telopodite curved, apically expanded, drawn out into long process on anterior edge of expanded tip. Posterior gonopods (Fig. 223): 5-segmented, typical of the genus. Coxae 10 and 11 and process of sternum 12 as in *C. crystallina.*

Description of female paratype. Length, 20 mm, A3 = 1.05 mm. Nonsexual characters as in male. Cyphopods (Figs. 224, 225): valves with high posterior carinae (Fig. 225); postgenital plate low, rounded (Fig. 224).

Distribution. Known only from the type locality. Many specimens have been collected by S. B. Peck, R. Mitchell, and others.

Notes. There is some variation in the pigmentation and number of ocelli. A few individuals have as few as 16 ocelli, irregular and not pigmented. Other specimens have about 20, regularly arranged and darkly pigmented; thus this species may be in the process of making the first morphological adaptations to a troglobitic existence. It has not been collected on the surface, though it has been searched for (S. Peck, personal communication). The type locality, Cueva de la Mina, has a remarkably diverse fauna of troglobitic arthropods for a tropical cave; there are two other millipeds (a cambalid and a glomerid), a scorpion, two pseudoscorpions, a mite, a campodean, a thysanuran, three beetles, a spider and an isopod (Mitchell, 1968).

THE *MACULATA* GROUP

In this large group, the colpocoxites are generally simple, long, and sharply bent posteriad about midlength. The telopodites are variable. Most species occur in the central highlands of Mexico and in the transverse volcanic belt.

Cleidogona maculata (Verhoeff) NEW COMBINATION

Figures 226–228

Mexiceuma maculatum Verhoeff, 1926, Zool. Anz., 68: 112, figs. 12–15, ♂.

Cleidogona leona Chamberlin, 1943, Bull. Univ. Utah, 34: 34, figs. 69–72, ♂. NEW SYNONYMY.

Cleidogona propia Causey, 1957, J. Kansas Entomol. Soc., 30: 119, figs. 13–14, ♂, 15, ♀. NEW SYNONYMY.

Types. Male holotype of *M. maculata* from Desierto de los Leones, near Mexico City, D. F., collected 20 July 1924 by Professor Dampf, in Zoologische Museum Munich, examined; male holotype of *C. leona* from Desierto de los Leones, in the University of Utah collection, examined; male holotype of *C. propia* from Puerto las Peras, on Highway 15, Michoacán, collected 15 June 1955 by D. Causey, in AMNH, examined. Puerto las Peras is not on any map seen by me and is not listed in Gazetteer 15 (Mexico), Official Standard Names approved by the United States Board on Geographic Names (1956).

Diagnosis. Distinct from other species of the group in the extent of the corrugations or rugae on the posterior face of the basal portion of the anterior gonopod colpocoxite (Fig. 226).

Description of male from type locality. Length, 15 mm, A3 = 0.80 mm. Ocelli 26, in 6 rows. Coloration typical. Segments cylindrical. Anterior gonopods (Figs. 226, 227): basal part of colpocoxites with numerous rugae or corrugations on anterior face, extending across entire width of gonopod. Coxae without projections, setose. Telopodites (Fig. 227) long, freely movable, apically divided, branches widely divergent. Colpocoxite in lateral view (Fig. 227) bent at slightly more than a right angle just beyond midlength. Posterior gonopods (Fig. 228): typical of genus; widest part of second segment just distal of midlength. Coxa 10 elongate, gland on long pedicel. Coxa 11 slightly enlarged above gland opening, lacking spine or plate. Process of sternum 12 typical.

Females have been collected, but none could be located for this study. The illustration by Causey (1957, fig. 15) shows the cyphopods to be very similar to those of *C. chontala* (Fig. 208).

Distribution. In addition to the type localities given for the various synonyms, the following: MICHOACÁN: Puerta Garnica, *ca.* 30 mi. east of Morelia, elev. 9200 ft., 30 July 1966, G. Ball and D. Whitehead, ♂.

Notes. Verhoeff's original illustration of the posterior gonopod does not agree with that of the type specimen. It is possible that he drew a regenerated appendage from another specimen. Chamberlin (1943) did not mention *C. maculata* in describing *C. leona;* Causey (1957) compared the specimens she described as *C. propia* to *C. nueva* Chamberlin.

Cleidogona tizoc n. sp.
Figures 229–231

Types. Male holotype from Delina, Pinal de Amoles, Querétaro, collected 10 July 1967 by J. Reddell. The species name is a noun in apposition, the name of an Aztec king, *ca.* 1481.

Diagnosis. Distinct from all other members of the *maculata*-group in having a prominent process on the anterior gonopod coxa (Fig. 230).

Description of male holotype. Length, 16 mm, A3 = 0.82 mm. Ocelli 25, in 6 rows plus single ocellus. Color typical. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 229), coxal knobs prominent; subapical process of colpocoxite extending distad from point of flexure. In lateral view (Fig. 230), coxa with acuminate, slightly curved process, setose. Apex of colpocoxite with a series of branches and processes, not simple as in *C. maculata* (compare Fig. 227); telopodites short. Posterior gonopods: coxa with a basal knob, small pointed process above knob (Fig. 231); second segment not much enlarged. Coxa 10 elongate; gland petiolate. Coxa 11 with small process above gland. Process of sternum 12 as usual.

Female unknown.

Distribution. In addition to the type locality: QUÉRETARO: 17.8 mi. east of Landa de Matamoros, 5300 ft. elev., S. and J. Peck, 4 July 1969, ♂♂.

Cleidogona zimapaniensis Causey
Figures 232–235

Cleidogona zimapaniensis Causey, 1957, J. Kansas Entomol. Soc., 30: 117, pl. 2, figs. 9–12, ♂♀.

Types. Male holotype and female paratype from 14 mi. north of Zimapán, Hidalgo, collected 23 June 1954 by N. Causey, in AMNH, examined.

Diagnosis. Distinct from all but *C. tizoc* in having a subapical process on the anterior part of the anterior gonopod colpocoxite, but differing from that species in lacking a coxal process.

Description of male holotype. In poor condition, broken into many pieces, A3 = 0.54 mm. Ocelli 27, in 6 rows. Coloration typical. Segments cylindrical. Anterior gonopods: in poor condition, basal parts destroyed, apparently cleared at one time, covered with sticky deposits partly cleaned away by ultrasonics. Only a line drawing can be presented here (Figs. 232–233), owing to the poor condition of the gonopods. Posterior gonopods: similar in form to those of *C. tizoc,* but basal process longer, with tiny knobs (Fig. 234); second segment wider than in *C. tizoc.* Coxa 10 elongate, gland on petiole. Coxa 11 with moderate lobes above gland. Process of sternum 12 short, rounded, with small thorn on basal part of ventral side.

Description of female paratype. Length, 15.5 mm, A3 = 0.80 mm. Nonsexual characters as in male. Cyphopods (Fig. 235): postgenital plate a narrow rod, somewhat expanded apically.

Distribution. Known only from the type locality.

Cleidogona camazotz n. sp.
Figures 236–238

Type. Male holotype and female paratype from 3 mi. west of Guerrero border, Guerrero, on Mexico Route 200, collected 14 July 1963 by J. Beatty and F. Coyle. The species name, a noun in apposition, refers to the bat monster of Mexican mythology.

Diagnosis. Like *C. maculata* and *C. bacillipus, C. camazotz* has prominent corrugations on the anterior basal part of the anterior gonopod colpocoxites (Fig. 236), but differs from *C. maculata* in having the corrugations less extensive (compare Fig. 226) and from *C. bacillipus* in the broader, more strongly curved colpocoxites.

Description of male holotype. Length, 21 mm, A3 = 0.80 mm. Ocelli 25 in 5 rows. Coloration typical, somewhat darker than usual. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 236), sternum broad, with short central fovea; colpocoxites with prominent outer ridge, corrugations limited to inner surfaces mesad of ridge. In lateral view, colpocoxite bent at right angle near midlength (Fig. 237), telopodite similar to that of *C. maculata.* Coxae 10 and 11 elongate, glands on petioles, knobs and processes absent. Process on sternum 12 typical.

Description of female paratype. Length, 19 mm, A3 = 0.80 mm. Nonsexual characters as in male. Cyphopods (Fig. 238): postgenital plate broadly triangular, apex rounded; valves lobed.

Distribution. In addition to the type locality: Oaxaca: 22.2 mi. south of San Pedro Juchatengo, near Pinotepa Nacional, 22 July 1966, G. Ball and D. Whitehead, ♂ ♀.

Cleidogona mayapec n. sp.
Figures 239–241

Types. Male holotype from 1 mi. south of Río Blanco, Querétaro, collected 8 July 1967 by J. Reddell. The species name is a noun in apposition, the name of the Lightning Dog of Mexican mythology.

Diagnosis. Lacks the corrugations present in the anterior gonopods of *C. maculata, C. camazotz* and *C. bacillipus;* differs from *C. tizoc* in lacking a coxal process.

Description of male holotype. Length, 9 mm, A3 = 0.47 mm. Ocelli 25 in 6 rows. Coloration typical. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 239), colpocoxites with ridge on median side. In lateral view (Fig. 240), colpocoxite bent at less than a right angle, nearly nearly touching telopodite. Posterior gonopods (Fig. 241): coxae with basal process long; second segment with widest part at midlength, almost subtriangular. Coxae 10 and 11 and sternal process 12 as described for *C. camazotz.*

Female unknown.

Distribution. In addition to the type locality, the following: (Querétaro: Cueva del Judio, 1 mi. south of Pinal de Amoles, 10 July 1967, J. Reddell, ♂.

Cleidogona xolotl n. sp.
Figures 242, 243

Types. Male holotype from 23.8 mi. northeast of Jacala, Hidalgo, elev. 5100 ft., collected 13 November 1965 by G. Ball and D. Whitehead. The species name (pronounced show-lotl) is a noun in apposition, the name of the brother of Quetzalcoatl.

Diagnosis. The unique form of the

telopodites (Fig. 242) immediately distinguishes this species from all others of the group.

Description of male holotype. Length, 20 mm, antennae missing. Ocelli 27 in 6 rows. Coloration typical. Segments cylindrical. Anterior gonopods (Fig. 242): colpocoxites bent at nearly a right angle, posterior side with acuminate, slightly curved process just distad to point of flexure, lateral apical margin drawn out, shieldlike. Telopodites small, weak, curved in nearly a circle, apex divided, branches widely diverging, small. Posterior gonopods (Fig. 243) with narrow basal processes on coxae; widest part of second segment distad of midlength. Coxae 10 typical. Coxae 11 with a large, thick plate projecting distad to gland. Process of sternum 12 typical, basally subglobose, apically pointed.

Female unknown.

Distribution. Known only from the type locality.

Cleidogona bacillipus (Chamberlin and Mulaik) NEW COMBINATION

Figures 244–247

Rhabdarona bacillipus Chamberlin and Mulaik, 1941, J. New York Entomol. Soc., 49: 60, no figures.

Mecistopus varicornis Loomis, 1959, J. Washington Acad. Sci., 49: 162, figs. 10–14, ♂. NEW SYNONYMY.

Types. Male holotype of *R. bacillipus* from Raven Ranch, Kerr Co., Texas, in University of Utah collection, examined; male holotype of *M. varicornis* from along Highway 16 between Kerrville and Medina, Texas, in USNM, examined.

Description of male holotype. Length, 18 mm, A3 = 0.75 mm. Ocelli 26 in 6 rows. Coloration typical. Segments cylindrical, lateralmost setae of segments on slightly raised knobs. Anterior gonopods: in anterior view (Fig. 244), colpocoxites narrow, upright, with lateral ridge limiting mesal corrugated or rugose area, apex of each colpocoxite turned slightly laterad; coxal knobs prominent. In lateral view (Fig. 245), colpocoxite bent at nearly a right angle beyond midlength, apex without complex processes; telopodite small, not apically divided. Posterior gonopods: coxa broadest at base, with large process slightly rugose distally; second segment clavate, widest at distal end; apical segment with a weak suture. Posterior gonopods giving the impression of being 4-segmented. Coxae 10 and 11 typical. Process of sternum 12 short, slightly decurved.

Description of female from near type locality. Length, 17 mm, A3 = 0.72 mm. Nonsexual characters as in male. Cyphopods (Fig. 247): postgenital plate with two projections.

Distribution. In addition to the type locality: UNITED STATES. TEXAS: (reported by Loomis, 1967) *Kerr-Bandera Cos.*, along road between Kerrville and Medina, 26 December 1958, H. and J. Loomis, ♂♂♀♀; *Comal Co.*, Landa Park, New Braunfels, 29 December 1958, H. and J. Loomis, ♂; *Kendall Co.*, 5 mi. south-southwest of Boerne, 31 January 1959, J. Loomis, ♂. MEXICO. NUEVO LEÓN: Monterrey, Chipinque Mesa, forest litter, elev. 5400 ft., 24 June 1969, S. and J. Peck, ♂♂♀♀; COAHUILA: 8.6 mi. east of San Antonio de las Alazanas, elev. 8200 ft., 21 October 1965, G. Ball and D. Whitehead, ♂♂♀♀.

Notes. The illustrations given by Loomis do not match the types of *M. varicornis* in several respects. In Loomis' figure 12 (Loomis, 1959) the gonopod telopodites are omitted; figure 13 shows an extra articulation above the coxal process of the posterior gonopod. Both *Rhabdarona* and *Mecistopus* were based mainly on the structure of the posterior gonopod, which, as can be seen in my Figure 246, is not very different from those of others in the *maculata*-group. This species has a wide distribution, the widest of any Mexican species. Perhaps it is more adapted to arid conditions than those found further south and has spread into areas in which it has no competition from congeners.

THE *GODMANI* GROUP

This group may not be a very natural one; part of it may be derived directly from the *crucis*-group, and another species may be more closely related to the *maculata*-group. The anterior gonopod colpocoxites of these species are simple, and some, like those of the species of the *maculata*-group, are abruptly bent about midlength, but in other species they are narrower, rodlike, and evenly curved. The telopodites are usually simple and unbranched. Species are found in Oaxaca, Veracruz, Guerrero, and Querétaro.

Cleidogona godmani Pocock
Figure 248

Cleidogona godmani Pocock, 1903, Biologia Centrali-Americana, Zoologia, Chilopoda and Diplopoda, p. 52, pl. 5, figs. 8a–c, ♂.

Hirsutogona godmani, Kraus, 1954, Senck. Biol., 35: 329.

Types. Male holotype from Omilteme (north of Zimpango), Guerrero, deposited in British Museum (Natural History), examined.

Diagnosis. The colpocoxites and telopodites (Fig. 248) of the anterior gonopods are the simplest of any species of the group, and the most sharply bent.

Description of male holotype. In poor condition; originally pinned and preserved dry, now in alcohol, bleached and stained green by corrosion from pin, all legs missing. Length, 17 mm, A3 = 0.65 mm. Ocelli 28, in 7 rows. Segments cylindrical. Anterior gonopods (Fig. 248): in anterior view, sternum broad at base, triangular, extending between colpocoxites. In lateral view, colpocoxite rodlike, apically expanded, bent at right angle; telopodite simple. Posterior gonopods: missing from holotype. Coxa 10 as usual. Coxa 11 with small, rounded cone distad of gland. Process of sternum 12 a short, triangular ridge.

Female unknown.

Distribution. Known only from the type locality.

Cleidogona tequila n. sp.
Figures 249–252

Types. Male holotype, female paratype and other specimens from Tequila (18° 44′ N, 97° 04′ W), Veracruz, collected 7 August 1967 by J. Reddell. The species name is a noun in apposition referring to the type locality.

Diagnosis. The long spatulate process on the coxae of the posterior gonopods (Fig. 251) resembles that of *C. totonaca* but lacks additional knobs.

Description of male holotype. Length, 11 mm, A3 = 0.63 mm. Ocelli 26, in 5 rows. Coloration typical. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 249), sternum extending between coxae and colpocoxites, coxal knobs prominent; colpocoxites with mesal ridge. In lateral view (Fig. 250), colpocoxite simple, evenly curved; telopodite with large, subterminal process. Posterior gonopods (Fig. 251) typical, but with long spatulate process from base of coxae. Coxae 10 and 11 and sternal process 12 as usual.

Description of female paratype. Length, 12 mm, A3 = 0.62 mm. Nonsexual characters as in male. Cyphopods (Fig. 252): valves with carinae, postgenital plate small.

Distribution. Known only from type locality.

Cleidogona hauatla n. sp.
Figures 253–256

Types. Male holotype and female paratype from 20 mi. west of Hauatla, Oaxaca, collected 10 August 1967 by J. Reddell, J. Fish, and T. Evans.

Diagnosis. The attenuate tip of the anterior gonopod colpocoxites is diagnostic (Fig. 254), as is the complexity of the posterior gonopod coxae (Fig. 255).

Description of male holotype. Length, 24 mm, A3 = 0.90 mm. Ocelli 26, in 5 rows plus single ocellus. Coloration typical. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 253), colpocoxites with definite lateral shoulders, as in *C. godmani* (compare Fig. 248); sternum broad, extending between colpocoxites, slightly depressed, with prominent anterior knobs. In lateral view (Fig. 254), colpocoxite narrow, evenly curved, tip acuminate. Telopodite apically broadened, bladelike. Posterior gonopods (Fig. 255) typical, but coxa with complex series of knobs, including vestigial gland opening on basal part, rugose area on distal part; widest part of second segment at distal end. Coxae 10 and 11 elongate, not otherwise modified. Process of sternum 12 a long rod.

Description of female paratype. Length, 24.5 mm, A3 = 0.90 mm. Nonsexual characters as in male. Cyphopods (Fig. 256): valves unmodified; postgenital plate broad, nearly square, transparent, with triangular teeth laterad to main plate.

Distribution. Known only from the type locality.

Cleidogona totonaca n. sp.
Figures 257–259

Types. Male holotype and other males from 17.8 mi. east of Landa de Matamoros, Querétaro, elev. 5300 ft., collected 18 November 1965 by G. Ball and D. Whitehead. The specific name is an adjective referring to the Totonac civilization of pre-Columbian Mexico.

Diagnosis. Closely related to *C. tequila*, but distinct in the form of the posterior gonopods (Fig. 295, compare Fig. 251).

Description of male holotype. Length, 20 mm, A3 = 0.90 mm. Ocelli 25 in 6 rows. Coloration typical. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 258), resembling those of *C. tequila*, but colpocoxites more divergent, ridge along midline rather than on mesal edge. In lateral view (Fig. 257), colpocoxite less curved; telopodite simpler than in *C. tequila*. Posterior gonopods as in Figure 259, apparently 6-segmented. Coxae 10 and 11 and process of sternum 12 all of typical form.

Female unknown.

Distribution. In addition to the type locality: QUERÉTARO: Sótano del Gobernador, 1 mi. south of Pinal de Amoles, 10 July 1967, J. Reddell, ♂.

THE *RAFAELA* GROUP

This group is clearly related to the *maculata*-group, but the colpocoxites are shorter, and, seen in lateral view, much broader in proportion to their length. The telopodites are generally simple and the posterior gonopods typical of the genus. *Cleidogona conotyloides* is a somewhat discordant element in this group, and may serve to relate the *rafaela*- and *godmani*-groups. Species of the *rafaela*-group occur in Chiapas, Oaxaca, and the vicinity of the Mexican Federal District.

Cleidogona rafaela Chamberlin
Figures 260–262

Cleidogona rafaela Chamberlin, 1943, Bull. Univ. Utah, 34: 35, figs. 73–75, ♂.

Types. Male holotype from San Rafael, "D. F.," deposited in University of Utah collection, examined. There seems to be no San Rafael in the Mexican Federal District; there is a San Rafael in Mexico State and San Rafael Zaragoza is in nearby Morelos.

Diagnosis. Distinct in details of the anterior gonopods (Fig. 260) from other species of the group.

Description of male holotype. Length, 15 mm, A3 = 0.54 mm. Ocelli 28 in 6 rows. Coloration typical. Segments cylindrical. Anterior gonopods (Fig. 260): broad in lateral view, posterior bladelike part of colpocoxite deeply indented near apex, margin concave; coxae setose; telopodite with small, lateral, subterminal tooth. Posterior gonopod: coxa elongate, with basal lobe, distal rugose area; widest part of second segment just beyond midlength. Coxa 10 elongate, gland nearly sessile. Coxa 11 with large chitinous plate above gland opening. Process of sternum 12 a small triangular ridge.

Description of female from type locality. Length, 15 mm, A3 = 0.57 mm. Nonsexual characters as in male. Cyphopods: valves with inner margins deeply sinuate (Fig. 262); postgenital plate apparently absent.

Distribution. Known only from the type locality.

Cleidogona zapoteca n. sp.

Figures 263–265

Types. Male holotype from San Pedro Juchatengo, near Pinotepa Nacional, Oaxaca, elev. 7100 ft., collected 23 March 1966 by G. Ball and D. Whitehead. The specific name refers to the Zapotec culture of pre-Columbian Mexico.

Diagnosis. Closest to *C. rafaela,* but distinct from that species in the oblique ridge across the anterior face of the anterior gonopod colpocoxites (Fig. 263) and the form of the anterior gonopod telopodite (Fig. 264, compare Fig. 260).

Description of male holotype. Length, 15 mm, A3 = 0.74 mm. Ocelli 26 in 5 rows plus single ocellus. Coloration typical. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 263), sternum not extending far between colpocoxites; coxae without setae. Colpocoxites with oblique ridge about midlength. In lateral view (Fig. 264) resembling gonopods of *C. rafaela,* but bladelike portion of colpocoxite with posterior margin convex, not concave; telopodite simple, pointed, not much curved. Posterior gonopods: typical of genus (Fig. 265). Coxae 10 and 11 and process of sternum 12 typical.

Female unknown.

Distribution. Known only from the type locality.

Cleidogona laquinta n. sp.

Figures 266–268

Types. Male holotype from 3 mi. east of San Cristóbal de las Casas, on road to La Quinta, Chiapas, collected 17 July 1956 by Bell and Van Horn. The species name refers to the type locality, and is a noun in apposition.

Diagnosis. This species resembles *C. conotyloides* in having moderately developed lateral shoulders, or paranota, though they are not as distinct as in that species. The gonopods are quite different, and more greatly resemble those of *C. zapoteca,* from which *C. laquinta* can be separated by its larger anterior gonopod telopodites (Fig. 268, compare Fig. 264).

Description of male holotype. Length, 9.5 mm, A3 = 0.47 mm. Ocelli 22 in 5 rows. Specimen bleached, but coloration probably as usual in fresh material. Segments with moderate paranota, somewhat less developed than those of *C. conotyloides* (Fig. 274), segments posterior of segment 17 roughly cylindrical. Anterior gonopods: in anterior view (Fig. 267), sternum extending between colpocoxites, coxae with only 2 setae; colpocoxites with a pronounced mesal ridge at the base, sharply curved apically. In lateral view (Fig 268) resembling gonopods of *C. zapoteca,* but telopodites bulkier, anterior margin of telopodite irregular. Posterior gonopods: typical (Fig. 266) but lacking a claw. Coxae 10 and 11 as usual, but coxae 11 without knobs; process of sternum 12 typical.

Female unknown.

Distribution. Known only from type locality.

Notes. This species, because of the moderate development of paranota, may serve to link the rest of the group with *C. conotyloides* (below), and through that species, with the *godmani*-group.

Cleidogona conotyloides n. sp.

Figures 269–274

Types. Male holotype from 8.6 mi. east of San Cristóbal de las Casas, Chiapas, 8500–9000 ft., collected 30 April 1966 by G. Ball and D. Whitehead; female paratype from 11.6 mi. north of Pueblo Nuevo, Chiapas, 5200 ft., collected 26 April 1966 by Ball and Whitehead.

Diagnosis. The very well-developed, *Conotyla*-like paranota distinguish this species from any other of *Cleidogona.*

Description of male holotype. Length, 16 mm, A3 = 0.54 mm. Ocelli 25 in 5 rows plus single ocellus. Coloration: paranota light, row of dark spots down midline of dorsum. Segments with well-developed paranota, similar to those found in members of the genus *Conotyla* (Conotylidae), 2 lateralmost setae of each side on paranota (Fig. 274). Anterior gonopods: in anterior view (Fig. 269), coxal knobs evident, colpocoxites closely appressed basally, simple, with mesal ridge. In lateral view (Fig. 270), colpocoxites simple, bladelike, slightly curved; telopodite apically expanded and sharply curved anteriad. Posterior gonopods: bulkier than is usual in genus, coxae with basal knob (Fig. 271). Coxae 10 and 11 elongate, with glands, not otherwise modified. Process of sternum 12 apically divided into 2 curved branches of equal length (Fig. 272).

Description of female paratype. Length, 15.5 mm, A3 = 0.50 mm. Nonsexual characters as in male. Cyphopods as in Figure 273.

Distribution. In addition to the type localities, an immature specimen from 5 mi. west of San Cristóbal de las Casas, Chiapas, 7200 ft., can probably be assigned to this species.

Notes. While the gonopods of this species are typical of *Cleidogona,* the strong paranota on the segments create a superficial resemblance to members of the family Conotylidae, not definitely known to occur south of Chihuahua. The cleft process of the twelfth sternum again demonstrates that this character is not of generic value, as Loomis (1966) supposed.

THE *STOLLI* GROUP

This small group of two species is intermediate between members of the preceding group and the Proto-*dybasia*-group, described below. The anterior gonopod colpocoxites give the impression of being small, blunt, and curved at a right angle. The telopodites are small (almost absent in *C. stolli*) and curved sharply dorsad. *Cleidogona mirabilis* is included in this group, despite the somewhat different appearance of the gonopod colpocoxites; it may belong to the Proto-*dybasia*-group, but the basal region of the anterior gonopods was evidently damaged during the original dissection. Species of the *stolli*-group occur in Chiapas, Mexico, and in Guatemala and El Salvador.

Cleidogona stolli Pocock
Figures 275–277

Cleidogona stolli Pocock, 1903, Biologia Centrali-Americana, Zoologia, Diplopoda et Chilopoda, p. 52, pl. 5, fig. 7a–e, ♂.

Hirsutogona stolli, Kraus, 1954, Senck. Biol., 35: 329.

Types. Male holotype and other specimens from Volcán de Agua, Guatemala, deposited in British Museum (Natural History), examined.

Diagnosis. The telopodites are the smallest of any *Cleidogona* species (Fig. 276), except *C. atoyaca,* in which they are absent.

Description of male holotype. Length, about 15 mm, all specimens in poor condition, originally pinned and dried; antennae and legs mostly missing. Ocelli 25, with no regular arrangement. Specimen bleached and stained green. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 275), sternum broad, not extending much between colpocoxites, coxal knobs prominent. Colpocoxites stout and simple. In lateral view (Fig. 276), colpocoxites curved at nearly a right angle, with shelflike apophysis above insertion of short, curved telopodites. Posterior gonopods absent from specimen. Coxae 10 with large, knobby cones above gland apertures. Coxae 11 as usual, chitinous shelves distad to glands. Process of sternum 12 typical.

Description of female from type locality. Length, about 15 mm, antennae missing. Cyphopods as in Figure 277, possibly distorted by drying and rehydration.

Distribution. Known only from the type locality.

Notes. This species is clearly related to *C. decurva,* and to *C. atoyaca* of the Proto-*dybasia*-group.

Cleidogona decurva n. sp.

Figures 278–280

Types. Male holotype from surface near Sumidero de Camino (a sumidero is a sinkhole with a stream running into it), 10 mi. northwest of Comitán, Chiapas, collected 22 August 1967 by J. Reddell.

Diagnosis. The anterior faces of the anterior gonopod colpocoxites are corrugated, as in some species of the *maculata*-group, but the short, decurved telopodites are distinctive.

Description of male holotype. Length, 12 mm, A3 = 0.61 mm. Ocelli 25 in 6 rows. Coloration typical. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 278) sternum not extending between colpocoxites, colpocoxites with prominent ridge, corrugated area mesal to ridge; colpocoxites apically expanded. In lateral view (Fig. 279), coxae large, with setae, extending around base of telopodites posteriorly; telopodites short, decurved, with two nearly right angles. Posterior gonopods: coxae complex, with series of basal lobes (Fig. 280); second joint very narrow at base, widest part just beyond midlength; apical joint rather longer than usual. Coxa 10 with cylindrical process above gland aperture. Coxa 11 typical. Process of sternum 12 suppressed, small elongate ridge.

Female unknown.

Distribution. In addition to the type locality: CHIAPAS: pine forest along Rt. 190, 8.5 mi. southeast of San Cristóbal de las Casas, 23 July 1956, R. T. Bell, ♂♂.

Cleidogona mirabilis (Kraus)

NEW COMBINATION

Figures 286, 287

Hirsutogona mirabilis Kraus, 1954, Senck. Biol., 35: 329, figs. 62–65, ♂.

Types. Male holotype and immature female paratype from Monte Cristo, Metapán Mts., Dept. Santa Ana, El Salvador, deposited in Senckenburg Museum, Frankfurt, examined.

Diagnosis. The details of the gonopods, in particular the rather thin colpocoxites, separate this species from others of the group.

Description of male holotype. Length, 18 mm, A3 = 0.86 mm. Ocelli 28 in 6 rows. Coloration typical. Segments cylindrical, segmental setae unusually stiff and short. Anterior gonopods: see Figure 286. The gonopods have been permanently mounted on microscope slides, so I can do little more here than present line drawings made with the aid of a microscope projecting device (Bioscope). The basal part of the gonopod has been destroyed, but the curved short telopodites indicate a relationship to *C. decurva* and *C. stolli.* Posterior gonopods: typical of the genus (Fig. 287), coxae with large basal knob, widest part of second segment near midlength; apical segment apparently divided, perhaps folded when mounted on slide. Coxae 10 and 11 and sternal process 12 as usual.

Distribution. Known only from the type locality.

THE PROTO-*DYBASIA* GROUP

I refer to this group as the Proto-*dybasia*-group rather than by the name of one of the included species, in order to emphasize its relationship to the genus *Dybasia,* of Panama. The two species belonging to this group are distinguished by the large knobs projecting from the sternum of the anterior gonopod. In species of *Dybasia,* these projections are usually free, and the sternum does not extend between the colpocoxites as it does in most species of *Cleidogona.* Showing further affinity with *Dybasia,* at least one species of this group has the telopodites reduced (a good observation of the telopodites was not possible in *C. minutissima*).

Cleidogona atoyaca Chamberlin

Figures 281–283

Cleidogona atoyaca Chamberlin, 1943, Bull. Univ. Utah, 34: 34, figs. 66–68, ♂.

Types. Male holotype from Atoyac, Veracruz, in University of Utah collection, examined.

Diagnosis. The only species of *Cleidogona* except *C. austrina* of Panama (see section on species not included in revision) that completely lacks anterior gonopod telopodites.

Description of male holotype. Length, 11 mm, A3 = 0.46 mm. Ocelli 20, arrangement somewhat irregular. Specimen bleached by long preservation. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 281), sternum with pair of subtriangular processes from portion between colpocoxites, depressed between processes; coxal knobs prominent, coxae setose; colpocoxites short, stout. In lateral view (Fig. 282), telopodites missing or reduced to small common knob at posterior bases of coxae. Posterior gonopods appearing 6-segmented, but apparent articulation just above coxal process may be artifact; coxal process long, with small knobs; widest part of second segment near midlength. Coxae 10 and 11 and process of sternum 12 as usual.

Female unknown.

Distribution. In addition to the type locality: VERACRUZ: Fortin de las Flores (as Fortin on most maps, near city of Orizaba), 26–30 June 1966, D. Whitehead, ♂.

Notes. This species has most of the characters used by Loomis (1964) to separate the genus *Acakandra* from *Cleidogona.* I have synonymized *Acakandra* under *Cleidogona,* but the only known male of *A. austrina,* the type and only species, lacks gonopods. The illustrations given by Loomis (1964) resemble *C. atoyaca,* but *C. austrina* occurs in Panama.

Cleidogona minutissima (Kraus)
NEW COMBINATION
Figures 284, 285

Hirsutogona minutissima Kraus, 1954, Senck. Biol., 35: 332, figs. 66–71, ♂.

Types. Male holotype from (shores of?) Laguna de las Ranas, Dept. Sonosante, El Salvador, deposited in Senckenburg Museum, Frankfurt, examined.

Diagnosis. This species has sternal processes on the anterior gonopods like those found in *C. atoyaca,* but, according to the illustrations of Kraus (1954), has much larger telopodites and a series of small teeth along the lateral edges of the colpocoxites (Fig. 284).

Description of male holotype. Length, 11 mm, A3 = 0.50 mm. Ocelli 25 in 5 rows. Coloration typical. Segments cylindrical. Anterior gonopods: see Figure 284 and Kraus (1954). The gonopods were mounted on a permanent microscope slide, much cleared and distorted by compression. The figure given here was made using a projection device (Bioscope). Posterior gonopods: much like those of *C. atoyaca* (Fig. 285, compare Fig. 283). Coxae 10 and 11 and sternum 12 as usual.

Female unknown.

Distribution. Known only from the type locality.

The North American Species of *Cleidogona*

KEY TO MALES OF NORTH AMERICAN *CLEIDOGONA* SPECIES

For species not included, see section above on species not included in revision.

1a. Posterior gonopod with large, conical process at base of coxa, nearly as large as rest of coxa (Fig. 246); San Antonio area of Texas .... *bacillipus* (discussed under Mexican species)
1b. Posterior gonopod without such a process 2
2a. Anterior gonopod telopodites with large, winglike lateral process (Fig. 350); Georgia .... *alata*
2b. Such a process lacking 3
3a. Posterior part of anterior gonopod colpocoxites enormously swollen; telopodites much reduced (Fig. 374); Ohio, Illinois .... *celerita*
3b. Not as above 4
4a. Each anterior gonopod colpocoxite divided nearly to base, anterior branch cupped; posterior, longer branch rodlike (Figs. 288–290); Big Bend region of Texas .... *chisosi*
4b. Anterior gonopod colpocoxites not divided, or if so, then only at apex, apical

branches not longer than one-third length of gonopod 5
5a. Divisions of anterior gonopod colpocoxite turned anteriad (Fig. 398); Indiana, Ohio to Kentucky, Virginia ...... *fustis*
5b. Divisions of anterior gonopod colpocoxites continuing line of colpocoxite, or curved posteriad; or gonopod colpocoxites not divided 6
6a. Anterior gonopod colpocoxites widely separated near base by sternum (Figs. 338, 342, 352, 359, 394) 7
6b. Anterior gonopod colpocoxites not widely separated at or near base by sternum (Figs. 297, 310, 320, 316, 332, etc.) 11
7a. Body length less than 10 mm; anterior gonopods as in Figs. 394, 395; Mississippi ...... *accretis*
7b. Body length more than 10 mm; anterior gonopods not as in Figs. 394–395 8
8a. Anterior gonopod colpocoxites apically divided 9
8b. Anterior gonopod colpocoxites not apically divided (Figs. 359, 360); North Carolina ...... *wrayi*
9a. Anterior gonopod telopodite with thornlike process below divided apex (Fig. 343); Virginia ...... *fidelitor*
9b. No such process 10
10a. Anterior gonopods as in Figs. 252, 253; Georgia ...... *georgia*
10b. Anterior gonopods as in Figs. 338, 339; North Carolina ...... *caroliniana*
11a. Anterior gonopod coxa with posterior process (Figs. 294, 311, 321, 333, 345, 368, 378) 12
11b. Anterior gonopod coxa lacking such a process (Figs. 302, 317, 329, 335, 364) 21
12a. Coxal process subtriangular, pointed (Figs. 311, 321, 368) 14
12b. Coxal process quadrate (Figs. 378–380, 386) 13
13a. Posterior branch of anterior gonopod colpocoxite apex distally notched, branches straight (Fig. 386); Arkansas ...... *laminata*
13b. Posterior colpocoxite branch not notched, apical branches curved posteriad (Figs. 378–380); see Map 12 ...... *caesioannulata*
14a. Anterior colpocoxites not apically divided (Figs. 307, 308); North Carolina ...... *lachesis*
14b. Anterior gonopod colpocoxites apically divided 15
15a. Posterior gonopod with large rodlike process on distal half of coxa (Fig. 312); North Carolina ...... *margarita*
15b. Posterior gonopod lacking such a process 16
16a. Anterior branch of anterior gonopod colpocoxite apex redivided (Figs. 320–323, 368) 17
16b. Anterior branch not redivided 18
17a. Posterior gonopod with deep basal coxal notch (Fig. 365); Mississippi ...... *mississippiana*
17b. Posterior gonopod as in Fig. 324; Virginia, North Carolina ...... *hoffmani*
18a. Apex of anterior gonopod telopodites deeply divided, clasping colpocoxites (Fig. 345); South Carolina ...... *steno*
18b. Apex of telopodites clublike (Figs. 294, 333) 19
19a. Coxal process of anterior gonopods wider at base than long (Fig. 333); Alabama ...... *tallapoosa*
19b. Coxal process of anterior gonopod not wider at base than long (Figs. 294, 298) 20
20a. Apical branches of anterior gonopod colpocoxite curved posteriad (Fig. 298); Map 13 ...... *inexpectata*
20b. Branches not curved (Fig. 294); Map 12 ...... *major*
21a. Anterior apical branch of colpocoxite completely redivided (Fig. 364), or rodlike and turned laterad (Figs. 370, 371) 22
21b. Not as above 23
22a. Anterior colpocoxite of anterior gonopod branch as in Fig. 364, Mississippi, Alabama ...... *grenada*
22b. Anterior colpocoxite branch of anterior gonopod as in Fig. 371; Louisiana *sublettei*
23a. Anterior gonopod colpocoxites not divided (Figs. 388–390); Illinois ...... *unita*
23b. Anterior gonopod colpocoxites apically divided 24
24a. Anterior gonopod telopodites with small winglike lateral process (Fig. 302); North Carolina ...... *nantahala*
24b. Such processes lacking 25
25a. Anterior gonopod with anterior colpocoxite branch a toothed lamella (Fig. 328); Georgia ...... *atropos*
25b. Not as above 26
26a. Gonopods as in Figs. 335–337; Florida ...... *hadena*
26b. Gonopods as in Figs. 316–318; North and South Carolina ...... *jocassee*

The *Chisosi* Group

Cleidogona chisosi Loomis
Figures 288–292

Cleidogona chisosi Loomis, 1963, J. Kansas Entomol. Soc., 36: 121, figs. 5–7, ♂.

Types. Male holotype from Pulliam Ridge, elev. 5400 ft., near Panther Basin, Big Bend National Park, Texas; female paratype from Green Gulch, road to Panther Basin, Big Bend National Park, Texas, deposited in USNM, examined.

Diagnosis. The form of the anterior gonopods, with the two-branched colpocoxites (Figs. 288–290) is unique in the genus.

Description of male holotype. Length, 9 mm, A3 = 0.50 mm. Ocelli 24 in 5 rows. Coloration typical. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 288), sternum with triangular extension between coxae; coxae with prominent lateral shoulders, setose. Colpocoxites with 2 branches, the anterior branch broad, mesally cupped, the posterior branch a long, flat lamella, longer than anterior branch and mesad to it (Fig. 289). In lateral view (Fig. 290), telopodite nearly half as long as posterior branch of colpocoxite, freely movable. Posterior gonopods: with three (four?) segments, resembling species of *Tiganogona;* coxa enlarged, depressed in median midline. Second segment not enlarged as is usual in *Cleidogona;* apical segments subglobose. Coxae 10 and 11 and sternal process 12 as usual in genus.

Description of female paratype. Length, 9 mm, A3 = 0.47 mm. Nonsexual characters as in male. Cyphopods (Figs. 292, 293): lateral valve extending posteriad of mesal valve (Fig. 293), curving mesad; postgenital plate (Fig. 292) low.

Distribution. Known only from the type localities.

Notes. Loomis' (1963) verbal description of the anterior gonopods is hard for me to follow, but he apparently did not recognize that the anterior gonopod colpocoxites of each side were divided into two branches. He may also have interpreted his figure of the gonopods in lateral view (Loomis, 1963, his fig. 6) while inadvertently reversing anterior and posterior. Loomis' figure 7 shows an extra articulation in the distal segments of the posterior gonopod.

THE *MAJOR* GROUP

This is the largest species group of *Cleidogona* in number of species, and probably represents the most actively speciating line in the genus; most of the present species probably originated when Pleistocene glacial conditions created isolated habitats in the southern Appalachians. The gonopods are very similar in most species. The anterior gonopod colpocoxites are apically divided, and there is usually a coxal process, found only in *C. tizoc* among the Mexican species. The telopodites are usually large and freely movable. The postgenital plate of females is often divided, and in typical species, each division has two branches (Fig. 296). The species clustered around *C. caroliniana* (see below) form a distinct subgroup, especially when the female genitalia are considered. *Cleidogona major* occurs from North Carolina to northern Virginia, but most other species of the group are to be found in limited areas of the central and southern Appalachians (Maps 12, 13).

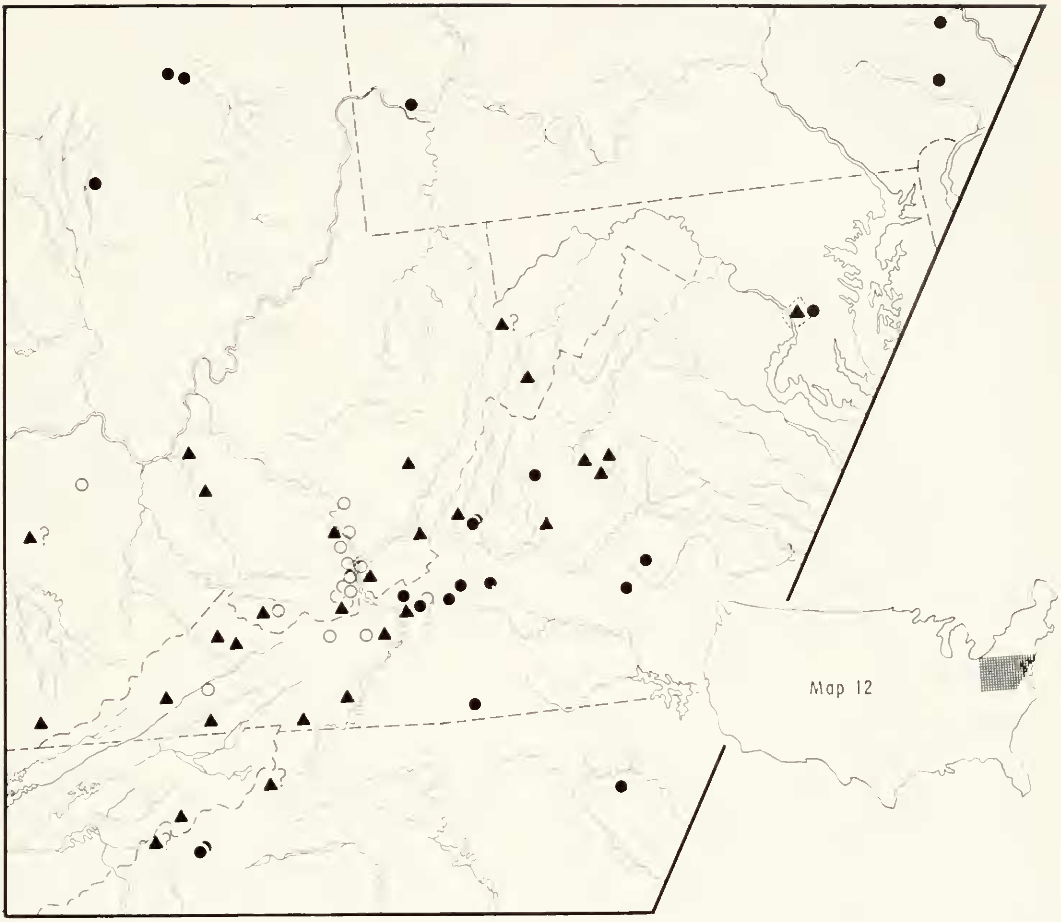
Cleidogona major Cook and Collins
Figures 294–296, Map 12

Cleidogona major Cook and Collins, 1895, Ann. New York Acad. Sci., 9: 47, figs. 110–137, ♂.

Types. Male holotype from Washington, D. C., in USNM, examined.

Diagnosis. Most closely related to *C. inexpectata,* but distinct from that species in the form of the coxal process and in the lesser apical curvature of the gonopod colpocoxites in *C. major* (compare Fig. 294, *C. major,* and Fig. 298, *C. inexpectata*).

Description of male holotype. Length, 20 mm, A3 = 0.95 mm. Ocelli 27 in 6 rows. Coloration typical. Segments cylindrical. Anterior gonopods: in lateral view, coxa swollen, coxal process squared off at tip, not curved; colpocoxites (Fig. 294) apically divided, branches subequal, neither branch shieldlike. Telopodites basally rodlike,



Map 12. West Virginia and parts of adjacent states, showing distribution of species of *Cleidogona*. Dots, *C. caesioannulata*; circles, *C. fustis*; triangles, *C. major*. *Cleidogona fustis* has also been reported from Indiana and Ohio.

broadly expanded apically, large and movable. Posterior gonopods (Fig. 295): typical of group, basal knob of coxa low, rounded; widest part of second segment just beyond midlength. Coxa 10 and 11 and sternal process 12 as usual.

Description of female from type locality. Length, 22 mm, A3 = 1.00 mm. Nonsexual characters as in male. Cyphopods: valves not modified; postgenital plate (Fig. 296) divided, each division with two branches, mesal branch longest and apically expanded, lateral branch broader at base, tapered, shorter.

Distribution (Map 12). Kentucky: *Bell Co.*, Pine Mt. State Park, 22 June 1950, R. Hoffman, ♂♀; *Powell Co.*, Natural Bridge State Park, 9 July 1966, B. Branson, ♂♀. North Carolina: (Dubious records, females only, may apply to *C. margarita*). *Madison Co.*, near Hot Springs, 6 July 1968, R. Hoffman, ♀; *Watauga Co.*, 6 mi. from Boone, 17 June 1948, M. Wright, ♀. Tennessee: *Carter Co.*, 4.5 mi. north of Shell Creek (3500 ft.), 17 July 1964, R. Hoffman, ♂. Virginia: *Albemarle Co.*, Stony Point, 30 October 1948, R. Hoffman, ♂♂♀♀; Saddle Hollow, March 1948, R. Hoffman, ♀; Charlottesville, November 1948, R. Hoffman, ♂♀; *Alleghany Co.*, 2 mi. northwest of Clifton Forge, 23 August 1947, R. Hoffman, ♂♀; *Buchanan Co.*, Grimleysville, 30 June 1951, R. Hoffman, ♂♀; 8 mi. southwest of Vansant, 1 July 1951, R. Hoffman, ♂; *Carroll Co.*, 9 mi. north of Fries, 10 June 1962, R. Hoffman, ♂; *Giles Co.*, 5 mi. west of Newport, 16 June 1962, R. Hoffman, ♂♀♀; *Grayson Co.*, west of Independence, 18 June 1950, R. Hoffman, ♀♀; *Pulaski Co.*, 10 mi. northeast of Pulaski, July 1963, D. Stapleton, ♂♂♀♀; *Rockbridge Co.*, Blue Ridge Parkway, Rocky Mount, 24 August 1949, R. Hoffman, ♂; *Scott Co.*, 3.5 mi. northeast of Dungannon, 31 July 1965, R. Hoffman, ♂; *Washington Co.*, 3 mi. northeast of Mendota, 31 July 1965, R. Hoffman, ♂♂. West Virginia: *Cabell Co.*, 2.5 mi. southeast of Ona, 12 August 1938, MacMillan and Richmond, ♂; *Greenbriar Co.*, Kate's Mt., above White Sulphur Springs, 5 April 1967, W. Shear, ♂♂; *Lincoln Co.*, Myra, 15 August 1948, Richmond, ♀; *McDowell Co.*, 5 July 1947, H. Hobbs, ♂; *Monroe Co.*, 2 mi. north of Ballard, 14 September 1962, R. Hoffman, ♀; *Mercer Co.*, Bluefield, 25 June 1966, R. Hoffman, ♂♂; *Pendleton Co.*, 3 mi. northeast of Franklin, 22 August 1958, L. Hubricht, ♂; *Raleigh Co.*, Grandview State Park, 14 September 1962, R. Hoffman, ♀; *Tucker Co.*, Parsons, Pernow Experimental Forest, 17 October 1965, J. and M. Cooper, ♀; *Webster Co.*, 5 mi. southwest of Three Forks, 18 June 1963, R. Hoffman, ♂♀.

Notes. Despite the wide range, there is little variation in this species, especially in the form of the gonopods. Cook and Collins (1895) suggested that this species might be the original of *C. caesioannulata*, even though they had just redescribed that species correctly.

Cleidogona inexpectata Hoffman
Figures 297–300, Map 13

Cleidogona inexpectata Hoffman, 1950, J. Elisha Mitchell Sci. Soc., 66: 22, figs. 23–25, ♂.

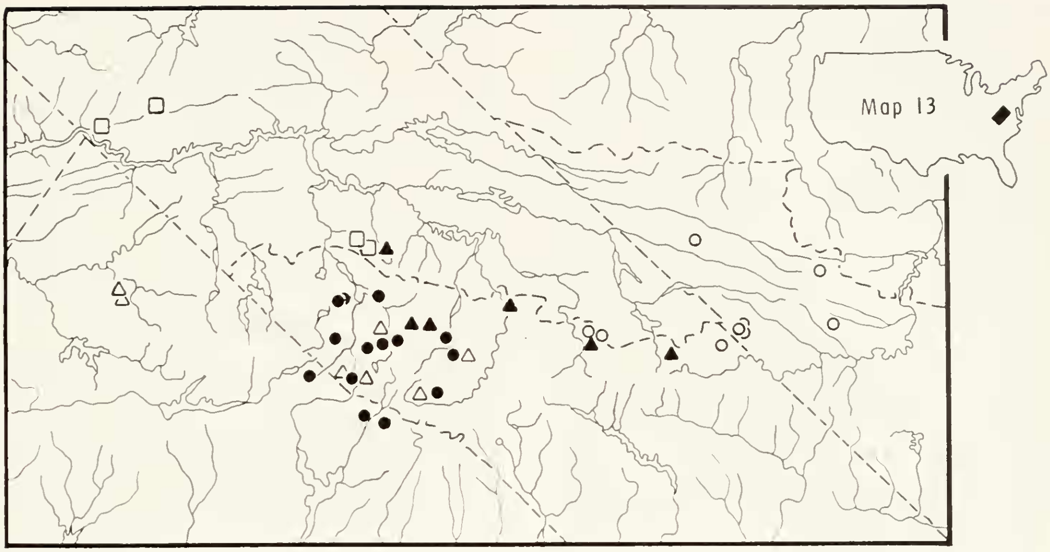
Types. Male holotype from Chimneys Camp Ground, Great Smoky Mountains National Park, Sevier Co., Tennessee, in USNM (Type No. 1878), examined.

Diagnosis. Closely related to *C. major*, but distinct from that species in the form of the coxal process of the anterior gonopods (Fig. 298) and the greater curvature in *inexpectata* of the apical part of the colpocoxites. The females of the two species may be separated by reference to Figure 296 (*C. major*) and Figure 300 (*C. inexpectata*).

Description of male from type locality. Length, 23 mm, A3 = 1.08 mm. Ocelli 30, in 7 rows plus single ocellus. Coloration normal. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 297), sternum extending well between colpocoxites, fused to colpocoxites; coxae setose, coxal knobs prominent. In lateral view (Fig. 298), colpocoxite apically divided, branches curved, posterior branch somewhat larger in lateral view, shieldlike; coxal process pointed, slightly curved; coxa depressed, not swollen as in *C. major*, depression limited by an anterior ridge. Telopodite similar to that of *C. major*. Posterior gonopods (Fig. 299): like those of *C. major*, but basal coxal process larger; second segment more evenly rounded on mesal edge. Coxa 10 elongate, gland on petiole. Coxa 11 with large shelf distad to gland opening. Process of sternum 12 a long rod, but of typical form.

Description of female from type locality. Length, 24.5 mm, A3 = 1.10 mm. Ocelli 29 in 7 rows on left side, like male on right side. Nonsexual characters as in male. Cyphopods: postgenital plate divided (Fig. 300), lateral branch of each division much reduced, mesal branch long, apically enlarged and lobed.

Distribution (Map 13). Tennessee: *Blount Co.*, Cades Cove Camp Ground, Great Smoky Mountains National Park, 29 August 1961, N. Causey, ♂♂♀♀; *Hamilton Co.*, Signal Mtn., 18 August 1956, R. Hoffman, ♂♂♀♀; *Sequatchie Co.*, 5 mi. southeast of Dunlap, 20 August 1956, R. Hoffman, ♂.



Map 13. Parts of Tennessee, North Carolina, Virginia, and Georgia, showing distribution of *Cleidogona* species. Dots, *C. jocassee*; circles, *C. hoffmani*; squares, *C. inexpectata*; open triangles, *C. nantahala*; solid triangles, *C. margarita*.

Notes. This species and *C. major* are very closely related and probably had a common ancestor in the recent past (late Pleistocene?). *Cleidogona inexpectata* is distributed to the south of *C. major* and has extended its range into the western Tennessee foothills. Undoubtedly many further localities for this species remain to be discovered.

Cleidogona nantahala n. sp.
Figures 301–306, Map 13

Types. Male holotype, female paratype, and other specimens from Mt. Pisgah, elev. 5000 ft., Haywood Co., North Carolina, collected 7 April 1949 by D. L. Wray. The specific name refers to the Nantahala National Forest.

Diagnosis. Related to *C. margarita, C. lachesis,* and *C. jocassee,* but distinct from those species in lacking a coxal process on the anterior gonopods (Fig. 302, compare Figs. 308, 311, and 317); females of *C. nantahala* do not have the postgenital plate divided as in *C. margarita* and *C. jocassee,* and the valves are modified. Females of *C. lachesis* are unknown.

Description of male holotype. Length, 17 mm, A3 = 0.72 mm. Ocelli 26 in 6 rows. Coloration pale, but typical, segments cylindrical. Anterior gonopods: in anterior view (Fig. 301), sternum broadly extended between coxae and colpocoxites, coxae elongate, with obvious knobs. In lateral view (Fig. 302), coxal process suppressed; colpocoxite apically divided, inner (posterior) branch bladelike, finely hirsute posteriorly, lateral (anterior) branch, expanded, shieldlike. Telopodite with short wing near midlength, slightly expanded apically, sharply curved. Coxa (Fig. 304) with swollen rugose area above gland aperture (note spermatophore on tip of extruded gland) on mesal side, blunt process on lateral side. Coxa 11 with small plate distal to gland. Process of sternum 12 (Fig. 305) typical, slightly larger distally than usual.

Description of female paratype. Length, 17 mm, A3 = 0.70 mm. Nonsexual characters as in male. Cyphopods (Fig. 306) with large, transparent, apically irregular processes posterior on lateral valves; postgenital plate not divided, flared broadly at tip, transparent.

Distribution (Map 13). NORTH CAROLINA: *Jackson Co.,* Western Carolina University Preserve, Cullowhee, 25 October 1969, W. Shear, ♂♀♀; *Macon Co.*, 5 mi. west of Highlands, 26 October 1969, W. Shear, ♂♂; Highlands, 16 November 1961, R. Hoffman, ♂♂♀♀; *Transylvania Co.*, Balsam Grove, 16 October 1965, R. Hoffman, ♂♂.

The following specimens are females that conform to Figure 306, but in the absence of males, I am reluctant to assign them for certain to *C. nantahala.* They are indicated on Map 13. GEORGIA: *Pickens Co.,* 2 mi. south of Marble Hill, 8 April 1961, L. Hubricht, ♀; 4 mi. north of Jasper, 6 November 1960, L. Hubricht, ♀.

Notes. The female genitalia of this species resemble those of species of the *alata*-group, to which it may be related; this interpretation is reinforced by the small "wing" on the anterior gonopod telopodite. *Cleidogona nantahala* is limited to the southern Blue Ridge.

Cleidogona lachesis n. sp.

Figures 307–309

Types. Male holotype from Linville Falls, Avery Co., North Carolina, 7 April 1949 by D. L. Wray. The species name, a noun in apposition, is the name of one of the three fates, and was suggested by the hooded appearance of the anterior gonopod colpocoxites.

Diagnosis. Related to *C. jocassee* and *C. margarita,* but distinct in having the inner (posterior) branch of the anterior gonopod colpocoxites suppressed and not visible in lateral view (Fig. 308). The posterior gonopods resemble those of *C. margarita,* but the apical process of the coxa is smaller.

Description of male holotype. Length, 19 mm, A3 = 0.90 mm. Ocelli 28–30 in 6 rows. Coloration typical. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 307), coxae without pronounced knobs, sternum extending between colpocoxites and fused to them. In lateral view (Fig. 308), coxa with rugose area below setae, coxal process pointed; colpocoxite with only outer branch visible, outer branch hoodlike, smooth, telopodites upright, expanded apically, not much curved. Posterior gonopods (Fig. 309): basal process of coxa small, subapical process rounded, of moderate size; widest part of expanded second joint just distad of midlength. Coxae 10 and 11 as usual. Process of sternum 12 short, pointed, not reaching beyond coxae 11.

Female unknown.

Distribution. In addition to the type locality: NORTH CAROLINA: *Avery Co.*, east side of Grandfather Mountain, 1 June 1954, R. L. Hoffman, ♂.

Cleidogona margarita Hoffman

Figures 310–315, Map 13

Cleidogona margarita Hoffman, 1950, J. Elisha Mitchell Sci. Soc., 66: 21, figs. 19–22, ♂♀.

Types. Male holotype and female paratype from Chimneys Camp Ground, Great Smoky Mountains National Park, Sevier Co., Tennessee, in USNM, examined.

Diagnosis. Closely related to *C. jocassee,* but distinct in the larger coxal process on the anterior gonopods (Fig. 311) and the presence of a long subapical rod on the coxae of the posterior gonopods (Fig. 312).

Description of male from Soco Gap. Length, 18 mm, A3 = 0.80 mm. Ocelli 31–33 in 6 rows. Coloration typical. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 310), with sternum extending between colpocoxites and expanded between them; coxal knobs prominent; anterior branch of colpocoxite shieldlike, concealing base of posterior branch. In lateral view (Fig. 311), coxal process large, quadrate, telopodite evenly and slightly curved, not much expanded apically. Posterior gonopods (Fig. 312), coxa with abortive gland knob basally, long rod subapically; second segment more evenly curved mesally than in other species, widest part near midline. Coxae 10 and 11 and sternal process 12 as described for *C. inexpectata* (Figs. 313, 314).

Description of female from Soco Gap. Length, 19 mm, A3 = 0.82 mm. Nonsexual characters as in male. Cyphopods (Fig. 315): postgenital plate poorly sclerotized, with two upright rods.

Distribution (Map 13). NORTH CAROLINA: *Haywood Co.,* Soco Gap, 23 September 1961, R. Hoffman, ♂♂♀♀; *Jackson Co.,* Soco Gap Falls, 20 May 1959, R. Hoffman, ♀; *Madison Co.,* Hot Springs area, 6 July 1968, R. Hoffman, ♂♀; *Mitchell Co.,* 3 mi. south of Bakersville on N. C. Rt. 226, 12 July 1962, R. Hoffman, ♂; *Watauga Co.,* 4 mi. north of Vilas on US 421, 11 July 1962, R. Hoffman, ♂♀. See also North Carolina records of *C. major.*

Cleidogona jocassee Hoffman
Figures 316–319, Map 13

Cleidogona jocassee Hoffman, 1950, J. Elisha Mitchell Sci. Soc., 66: 19, figs. 15–18, ♂♀.

Types. Male holotype and female paratype from Jocassee, Oconee Co., South Carolina, in USNM (Type No. 1876), examined.

Diagnosis. The general appearance of the anterior gonopods is very much like that of *C. margarita,* but the coxal process is much suppressed (Fig. 317).

Description of male holotype. Length, 21 mm, A3 = 1.00 mm. Ocelli 27 in 6 rows plus single ocellus. Coloration typical. Segments cylindrical. Anterior gonopods (Figs. 316, 317): as in *C. margarita,* but coxal process suppressed, reduced to low rounded swelling; telopodites more abruptly expanded apically, not as curved as in *C. margarita.* Posterior gonopods (Fig. 318): typical of genus; widest part of second segment subapical. Coxae 10 and 11 and sternum 12 typical.

Description of female paratype. Length, 22.5 mm, A3 = 1.00 mm. Nonsexual characters as in male. Cyphopods: typical of group, postgenital plate divided (Fig. 319), with branches not as deeply separated as in *C. inexpectata* or *C. major.*

Distribution (Map 13). GEORGIA: *Rabun Co.,* Glade Mtn., 27 July 1949, R. Hoffman, ♀♀. NORTH CAROLINA: *Haywood Co.,* Lake Junaluska, 6 July 1959, H. Weems, ♂♀; Mt. Pisgah, 4000–5000 ft., 4 July 1959, H. Weems, ♂♂♀♀; *Jackson Co.,* Cullowhee, 25 October 1969, W. Shear, ♀♀; Balsam, 3 August 1949, R. Hoffman, ♂; Chatooga River Gorge, 1 August 1958, R. Hoffman, ♂♀; *Macon Co.,* Wayah Bald, 5335 ft., 13 June 1953, R. Hoffman, ♂♂♀♀; 5 mi. north-northwest of Highlands, 9 July 1958, R. Hoffman, ♂♂♀♀; *Swain Co.,* base of Cliff Ridge at Nantahala, 6 May 1951, L. Hubricht, ♂♂♀♀; 3.3 mi. northeast of Nantahala, 16 May 1961, L. Hubricht, ♂♀; Birdtown, 6 May 1961, L. Hubricht, ♂♂♀♀; *Transylvania Co.,* Pink Beds Recreation Area, 8 mi. north of Brevard, 28–30 July 1958, R. Hoffman, ♂♂♀♀. SOUTH CAROLINA: *Oconee Co.,* Chatooga River, 2 mi. north of Mountain Rest, 22 July 1958, R. Hoffman, ♂.

Cleidogona hoffmani n. sp.
Figures 320–327, Map 13

Types. Male holotype, female paratype and other specimens from Roan Mt., below Carvers Gap, Mitchell Co., North Carolina, collected 23 September 1950 by Leslie Hubricht. The species name honors Dr. Richard L. Hoffman, in recognition of his many contributions to North American diplopod taxonomy, and his indispensable help with this study.

Diagnosis. Related to *C. margarita, C. jocassee,* etc., but differing in having the posterior branch of the apex of the anterior gonopod colpocoxite subdivided (Figs. 321–323).

Description of male holotype. Length, 18 mm, A3 = 0.75 mm. Ocelli 23–25 in 6 rows. Coloration typical. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 320), sternum extending between colpocoxites, fused to them; coxal knobs moderate. Anterior faces of colpocoxites with 2 ridges, mesal and lateral. In lateral view (Fig. 321) coxal process slightly curved, nearly triangular. Posterior branch of apex of colpocoxite flattened, posteriorly finely laciniate; anterior branch divided, lateralmost division rodlike, curved, mesal division somewhat flattened. Telopodite apically expanded and cupped, curved anteriad about two-thirds from base. Posterior gonopods (Fig. 324): not as highly modified as others in group. Coxae 10 as usual. Coxa 11 (Fig. 325) with small lamina distad to gland. Process of sternum 12 as usual, posterior ridge of sternum with two small knobs.

Description of female paratype. Length, 18 mm, A3 = 0.72 mm. Nonsexual characters as in male. Cyphopods (Figs. 326, 327): valves modified, with thin lamina ventrally (Fig. 327); postgenital plate typical of genus, much like that of *C. jocassee*, but mesal branch of each division longer, divisions not so deeply divided.

Distribution. All collections by R. Hoffman. NORTH CAROLINA: *Ashe Co.*, 3 mi. northwest of Lansing, 13 October 1963, ♂♂♀♀. TENNESSEE: *Carter Co.*, top of Roan Mt., 22 June 1950, ♂♀. VIRGINIA: *Bland Co.*, Hamilton Cave, 3 mi. northeast of Mechanicsburg, 9 September 1956, ♂; *Grayson Co.*, Mt. Rogers, 4500 ft., 12 and 27 September 1962, ♂♂♀♀; Helton Creek, east side of Mt. Rogers, 1 June 1950, ♂; south slope of Mt. Rogers, 20 October 1963, ♂♂♀♀; *Russell Co.*, 1 mi. northwest of Lynn Springs, 20 April 1962, ♂; *Tazewell Co.*, north side of Beartown Mtn., 25 August 1969, ♂♂♀♀; East River Mtn., 11 September 1955, ♂♀; *Wythe Co.*, Reed Creek at Carter Wayside, Ft. Chiswell, 4 October 1969, ♂♂.

Notes. This species has been collected in beech woods and on the muddy banks of a stream. There is some variation in the male gonopods; a male from Beartown Mountain (Fig. 323) has the posterior branch of the gonopod apex less curved. Specimens from Mt. Rogers, Virginia, have the colpocoxites shorter beyond the coxal process (Fig. 322), and differ slightly in the tip of the colpocoxite as well.

Cleidogona atropos n. sp.

Figures 328–331

Types. Male holotype and female paratype from 1 mi. south of Munnerlynn Swamp, Burke Co., Georgia, collected 24 October 1959, by L. Hubricht. The specific name is a noun in apposition, the name of one of the three fates.

Diagnosis. The details of the gonopods (Figs. 328–329) distinguish this species from others of its group. The female genitalia resemble those of *C. nantahala* and *C. steno*, but can be separated by reference to the figures.

Description of male holotype. Length, 10.5 mm, A3 = 0.54 mm. Ocelli 24 in 6 rows plus single ocellus. Coloration probably typical in fresh material, types bleached by preservation. Segments cylindrical. Anterior gonopods: tips of colpocoxites in anterior view (Fig. 328) with posterior branches thin plates, marginally dentate, the teeth irregular, posterior branches sinuously curved. In lateral view (Fig. 329), coxa without a process, setae in two groups; colpocoxite with posterior apical branch heavily laciniated along posterior margin. Telopodite sigmoidally curved, apically swollen. Posterior gonopods (Fig. 330) typical. Coxae 10 as usual. Process of coxa 11 reduced in size. Process of sternum 12 as usual.

Description of female paratype. Length, 11 mm, A3 = 0.55 mm. Nonsexual characters as in male. Cyphopods (Fig. 331): valves with posterior carinae; postgenital plate slightly narrowed at base, rounded distally, but with sharp corners.

Distribution. Known only from the type locality.

Notes. This species, *C. nantahala*, *C. steno*, *C. caroliniana*, *C. georgia* and possibly *C. tallapoosa* and *C. fidelitor* form a subgroup within the *major*-group connecting the species more typical of the group to the species of the *alata*- and *missis-*

sippiana-groups. It is difficult to place species either in this subgroup or in the *alata*-group; the female genitalia indicate an affinity with the *alata*-group.

Cleidogona tallapaosa n. sp.

Figures 332–334

Types. Male holotype and several other males from 4 mi. south of Perryville, Tallapoosa Co., Alabama, collected 24 July 1960 by L. Hubricht. The specific name refers to the type locality.

Diagnosis. A rather typical species of the *major*-group, despite its far southern distribution. A comparison of the figures of the anterior gonopods is necessary to distinguish this species from the group of species near *C. margarita.*

Description of male holotype. Length, 20 mm, A3 = 0.90 mm. Ocelli 30 in 7 rows. Coloration typical, slightly paler than usual, yellow-white marked medium tan to brown. Segments typical. Anterior gonopods: in anterior view (Fig. 332), sternum extending between coxae, rounded above, deep fissure in midline; coxal knobs prominent. In lateral view (Fig. 333), coxal process triangular, not curved; apical branches of colpocoxite with posterior branch flattened, laciniate, anterior branch shieldlike, twisted mesad. Telopodite not curved, upright, apically enlarged. Coxae 10 typical, glands on short pedicels. Coxae 11 as usual; process of sternum 12 shaped as usual, but somewhat longer, extending more ventrad than in other species.

Female unknown.

Distribution. Known only from the type locality.

Cleidogona hadena Causey

Figures 335–337

Cleidogona hadena Causey, 1961, Florida Entomol., 44: 38, figs. 3, 4, ♂.

Types. Male holotype from Juniper Springs, Marion Co., Florida, in AMNH, examined. The species name may be an acronym for H. A. Denmark.

Diagnosis. The anterior prong of the bifid tip of the anterior gonopod colpocoxite is reduced; the dividing notch between the two branches is not deep (Fig. 335). This is the only species of the *major*-group occurring in Florida.

Description of male holotype. Length, about 16 mm, A3 = 0.70 mm. Ocelli 24 in 6 rows. Coloration typical. Segments cylindrical. Anterior gonopods: probably had been cleared in corrosives or enzymes, basal portion could not be studied in detail. An anterior view of colpocoxite tip (Fig. 336) shows relationship of two branches of apex. In lateral view, distal parts of gonopod (Fig. 335) show coxal process below insertion of telopodite, telopodite distally bifid, sigmoidally curved. Posterior gonopods (Fig. 337) typical of family. Coxae 10 and 11 as usual. Sternal process 12 shorter than usual, with a small dorsal hook.

Female unknown.

Distribution. Known only from the type locality.

Cleidogona caroliniana Causey

Figures 338–340

Cleidogona caroliniana Causey, 1957, J. Kansas Entomol. Soc., 30: 115, figs. 4, 5, ♂.

Types. Male holotype from Fayetteville, Cumberland Co., North Carolina, in AMNH, examined.

Diagnosis. Differs from others of the *major*-group in lacking a coxal process (Fig. 339) and in having the telopodite apically divided, the branches widely diverging. The similar *C. fidelitor* (Fig. 343) has a small subterminal tooth on the anterior gonopod colpocoxites. *Cleidogona steno* (Fig. 345) has a coxal process.

Description of male holotype. Length, 10.5 mm, A3 = 0.60 mm. Ocelli 25 in 6 rows. Coloration typical. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 338), colpocoxites widely separated at base by extension of sternum; processes from basal articulations of telopodites clearly visible; coxal knobs prominent. In lateral view (Fig. 339), coxa without process; colpocoxites apically divided, anterior branch shieldlike. Telopodites sigmoidally curved, apically divided, branches curved and widely diverging, clasplike. Posterior gonopods (Fig. 340): typical of genus. Coxae 10 and 11 as usual; sternal process 12 as described for *C. hadena.*

Female unknown.

Distribution. Besides the type locality: SOUTH CAROLINA: Sumter Co., 2 mi. south of Edgefield, 22 November 1959, L. Hubricht, ♂.

Notes. The above record and type locality suggest a wide distribution for this species.

Cleidogona fidelitor n. sp.
Figures 341–343

Types. Male holotype from Mt. Tory Furnace, Lyndhurst, road to Sherando, Augusta Co., Virginia, collected 27 November 1965 by K. Brownell. The name is a noun in apposition, meaning "loyalist" and refers to the type locality.

Diagnosis. In anterior view, the anterior gonopods resemble those of *C. caroliniana,* in having basal processes from the telopodites visible (Fig. 342); however, *C. fidelitor* has much larger telopodites with a small subterminal tooth (Fig. 343). The segments also have moderately developed shoulders.

Description of male holotype. Length, 11 mm, A3 = 0.63 mm. Ocelli 26 in 5 rows. Coloration pale, typical pattern seen only on anterior segments. Segments with moderately developed shoulders bearing outer setae. Anterior gonopods: in anterior view (Fig. 342), sternum broad, widely separating colpocoxites, between which protrude processes from bases of telopodites; coxal knobs prominent. In lateral view (Fig. 343), coxa lacking process, setose; anterior branch of divided colpocoxite apex shieldlike, turned laterad; posterior branch heavily laciniate on posterior margin. Telopodite very large, curving anteriad, with subterminal tooth, terminal divisions of telopodite cupped around posterior colpocoxite branch. Posterior gonopods (Fig. 341): typical of genus. Coxa 10 with gland not on a petiole. Coxa 11 with small plate above gland opening. Process of sternum 12 typical.

Female unknown.

Distribution. In addition to the type locality: VIRGINIA: Bedford Co., Peaks of Otter, October 1960, R. Hoffman, ♂.

Cleidogona steno n. sp.
Figures 344–348

Types. Male holotype, female paratype, and a second female from Burnt Mountain, Pickens Co., Georgia, collected 6 November 1960 by L. Hubricht. The species name, a noun in apposition, is the name of one of the three gorgons.

Diagnosis. This species somewhat resembles *C. fidelitor* when the gonopods are seen in lateral view (Fig. 345), but there is a coxal process in *C. steno,* and in anterior view (Fig. 344) no basal telopodite process is seen.

Description of male holotype. Length, 14.5 mm, A3 = 0.80 mm. Ocelli 27 in 5 rows plus a single ocellus. Coloration pale but typical, specimens may be bleached by preservative. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 344), coxal knobs very prominent; sternum not much extended between colpocoxites; colpocoxites with anterior apical branch shieldlike, posterior branch with process at base visible only in anterior view. In lateral view (Fig. 345), coxa with large, blunt process, telopodites sharply sigmoidally curved, embracing posterior colpocoxite branch as in *C. fidelitor.* Posterior gonopods (Fig. 346) typical of genus. Coxa 10 (Fig. 347) with rugose knob just above gland opening, lateral knob near apex. Coxa 11 as usual. Sternal process 12 typical, somewhat shorter than in other species of the group.

Description of female paratype. Length, 14 mm, A3 = 0.80 mm. Nonsexual characters as in male. Cyphopods (Fig. 348):

typical of subgroup (see *Notes* under *C. atropos*); lateral valves with very large, irregularly serrate posterior lamella; postgenital plate broadly expanded apically, deeply notched, transparent.

Distribution. Known only from the type locality.

THE *ALATA* GROUP

This group is difficult to separate from the last few species discussed under the *major*-group, and they probably represent a continuation of the same series of evolutionary trends. However, as a rule, the anterior gonopod colpocoxites of species of the *alata*-group are thinner in lateral view than those of the *major*-group, and the apical division of the colpocoxites is not so pronounced. The telopodites are large and freely movable, and usually curved. Females are known only for *C. georgia*, and the genitalia resemble those of *C. steno* and others (see above). Species of this group occur in the Piedmont and Atlantic Coastal Plain.

Cleidogona alata Causey
Figures 349–351

Cleidogona alata Causey, 1961, Florida Entomol., 44: 38–39, figs. 5–7, ♂.

Types. Male holotype from 1 mi. south of Ila, Madison Co., Georgia, in AMNH, examined. The species name probably refers to the winglike processes on the anterior gonopod telopodites.

Diagnosis. This species may be separated from all others by the upright, rodlike anterior gonopod colpocoxites and the large telopodites, with lateral flaring lamellae (Fig. 350).

Description of male holotype. Length, about 17.5 mm (data from Causey, 1961, holotype vial does not contain complete specimen), A3 = 0.72 mm. Ocelli 27, somewhat irregular in arrangement, about 6 rows. Coloration light, but typical. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 349), sternum extending between colpocoxites; coxal knobs prominent; colpocoxites with anterior apical branch, small, lamellate, sometimes toothed. In lateral view (Fig. 350), coxa without process; colpocoxite upright, rodlike, only slightly curved, posterior apical part very heavily laciniate. Telopodite large, bulky, readily movable, apically divided, but branches not widely diverging, with broad lateral winglike lamellae on lateral side of each telopodite. Posterior gonopods nearly exactly like those of *C. wrayi* (Fig. 361). Coxa 10 with gland not on pedicel, rugose knob above gland, lateral knob as a thick shelf. Coxa 11 as usual. Process of sternum 12 as in Figure 356.

Female unknown.

Distribution. Known only from the type locality.

Notes. Only the anterior portions of the holotype are to be found in the vial so labelled; the posterior segments in the vial are much larger and obviously belong to another species; the total segment number of the two fragments is more than 30.

Cleidogona georgia n. sp.
Figures 352–358

Types. Male holotype, female paratype and another female from 4.2 mi. southeast of Cochran, Bleckley Co., Georgia, collected 5 December 1959 by L. Hubricht. The species name refers to the type locality and is a noun in apposition.

Diagnosis. Distinct from *C. alata* in lacking the lateral lamellae on the anterior gonopod telopodites, and from *C. wrayi* in having the colpocoxites apically divided.

Description of male holotype. Length, 13 mm, A3 = 0.72 mm. Ocelli 22–23 in 5 rows. Coloration probably typical in fresh material, specimen bleached by preservation. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 352) with colpocoxites touching near bases, but slightly divergent distally; coxal knobs prominent; sternum with two large lateral lobes. Anterior apical branches of colpocoxites shieldlike. In lateral view (Fig.

353), coxa without process; posterior apical branch of colpocoxite with laciniate part on a knob; telopodite sigmoidally curved, smaller than in *C. alata,* apically divided, without lateral processes. Posterior gonopods: typical of genus (Fig. 354). Coxa 10 as in Figure 355; coxa 11 as in Figure 356. Process of sternum 12 typical in shape, but shorter and stouter than usual in genus (Fig. 357).

Description of female paratype. Length, 13.5 mm, A3 = 0.75 mm. Nonsexual characters as in male. Cyphopods (Fig. 358): valves with posterior lamellae with irregular edges; postgenital plate as in related species, but not notched as in *C. steno.*

Distribution. Known only from the type locality.

Cleidogona wrayi Causey
Figures 359–361

Cleidogona wrayi Causey, 1957, J. Kansas Entomol. Soc., 30: 114, figs. 1–3, ♂.

Types. Holotype male from Acre, Beaufort Co., North Carolina, in AMNH, examined.

Diagnosis. Distinct from other species of the group in having the anterior gonopod colpocoxites not divided apically.

Description of male holotype. Length, probably about 17–18 mm (specimen fragmented), antennae missing. Ocelli 28 in 6 rows. Coloration as usual. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 359), colpocoxites broadly separated by sternal extension, processes from bases of telopodites just visible in gap; coxal knobs prominent. In lateral view (Fig. 360), apex of colpocoxite not divided, sigmoidally curved, slightly expanded; telopodite sigmoidally curved, small subapical process present. Posterior gonopods (Fig. 361) as usual. Coxae of legs 10 and 11 as usual; sternal process 12 typical.

Females unknown.

Distribution. Known only from the type locality.

The *Mississippiana* Group

Species of this group are distinct from the *major*-group and *alata*-group in that the anterior branch of the apex of the anterior gonopod colpocoxites is elaborated into a process, sometimes with branches itself, that curve laterad and dorsad when the gonopod is *in situ.* The telopodites are generally large and apically expanded. Species of the group are found in extreme southern Alabama, northern Louisiana, and central Mississippi. They may be most closely related to the *caesioannulata*-group.

Cleidogona grenada n. sp.
Figures 362–367, 369

Types. Male holotype and female paratype, with several other specimens, from 3.4 mi. east of Grenada, Grenada Co., Mississippi, collected 21 August 1960 by L. Hubricht. The species name refers to the type locality.

Diagnosis. Cleidogona sublettei has only a single branch developed from the anterior part of the colpocoxite apex (Fig. 371); *C. mississippiana* (Fig. 368) has a coxal process, but otherwise is close to *C. grenada.*

Description of male holotype. Length, 16 mm, A3 = 0.74 mm. Ocelli 29 in 6 rows. Coloration typical. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 362), sternum broad, fused to colpocoxites; coxal knobs not prominent. Anterior branch of colpocoxite apex extending nearly at right angles to body of colpocoxite. In lateral view (Figs. 363, 364), colpocoxite apex with posterior branch rodlike, laciniate (Fig. 364), anterior branch subdivided into 2 or 3 parts, one extending laterally, a second apically and a third ventrally (compare Fig. 363); telopodite large, apically expanded, not divided; coxal process absent. Posterior gonopods: coxa with acuminate basal process below a notch, distal face of notch rugose; second segments not much swollen, widest part just beyond midlength. Coxa 10 as usual. Coxa 11 as in Figure 366 (note spermatophore on extruded gland). Sternal process 12 as in Figure 367, typical.

Description of female paratype. Length, 14 mm, A3 = 0.72 mm. Nonsexual characters as in male. Cyphopods with postgenital plate divided (Fig. 369), margins irregularly toothed.

Distribution. In addition to the type locality: ALABAMA: *Mobile Co.,* Mobile, 11 September 1959, W. Suter, ♂♂♀♀.

Notes. The ventrally pointing part of the anterior colpocoxite branch is easily broken off (compare Figs. 363, 364, drawn from two different specimens from the type locality). In all features, this species is nearly identical to *C. mississippiana,* but the presence of a coxal process in *C. mississippiana* separates the two species. There are also some differences in the apex of the anterior gonopod colpocoxites (compare Figs. 364 and 368). However, it is clear that these two species are very closely related, and they may have to be synonymized if intermediate specimens are collected.

Cleidogona mississippiana Chamberlin
Figure 368

Cleidogona mississippiana Chamberlin, 1942, Bull. Univ. Utah, 32: 3, figs. 4–6, ♂.

Types. Male holotype from 8 mi. east of Vicksburg, Warren Co., Mississippi, in University of Utah Collection, examined.

Diagnosis. Closely related to *C. grenada,* but differs in that *C. mississippiana* (Fig. 368) bears a coxal process on the anterior gonopods.

Description of male holotype. Length, 20 mm, A3 = 0.90 mm. Ocelli 29 in 6 rows. Coloration typical. Segments cylindrical. Anterior gonopods: almost exactly as in *C. grenada,* but differing in having a coxal process and in the details of the apical branches, as shown in Figure 368. Posterior gonopod: exactly as in *C. grenada* (Fig. 365). Coxae 10 and 11 and sternal process 12 as usual.

Females have been collected but none could be obtained for study.

Distribution. As reported by Chamberlin (1942): MISSISSIPPI: *Rankin Co.,* Roosevelt State Park, 20 August 1940, S. Mulaik, ♂♀; *Forest Co.,* 14 mi. west of Forest, 26 August 1940, S. Mulaik, ♂.

Notes. See *Notes* section under *C. grenada.*

Cleidogona sublettei Causey
Figures 370–373

Cleidogona sublettei Causey, 1954, Tulane Stud. Zool., 2: 66, figs. 4, 5, ♂.

Types. Male holotype from Grand Ecore, Natchitoches Parish, Louisiana, in AMNH, could not be located.

Diagnosis. Distinct from both *C. grenada* and *C. mississippiana* in the shorter anterior gonopod telopodites and simple anterior apical colpocoxite branch (Fig. 371).

Description of male from Natchitoches, La. Length, 19 mm, A3 = 0.80 mm. Ocelli 29 in 7 rows. Coloration typical. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 370), much as in *C. grenada,* sternum not as broad as in *C. grenada.* In lateral view (Fig. 371), coxal process absent; colpocoxite anterior apical branch single, turned laterad; posterior branch rodlike. Telopodite shorter than in *C. grenada,* apically swollen and truncate. Posterior gonopods (Fig. 372) similar to *C. grenada* and *C. mississippiana,* but basal coxal knob smaller. Coxae 10 and 11 and sternal process 12 as usual.

Description of female from Natchitoches, La. Length, 20 mm, A3 = 0.84 mm. Nonsexual characters as in male. Cyphopods (Fig. 373): valves with large anterior hooks; postgenital plate divided, much like that of *C. grenada* (Fig. 369).

Distribution. In addition to the type locality: LOUISIANA: *Natchitoches Par.,* Natchitoches, 26 October 1954, C. Sublette, ♂♀.

THE *CAESIOANNULATA* GROUP

This northern and western offshoot from the *major*-group is characterized by having the coxal process of the anterior gonopods developed into a more or less broad plate, or having the posterior faces of the colpocoxites and coxae greatly swollen. The telopodites are moderately large to very small (in *C. celerita*). The female genitalia resemble those of species of the *major*-group very closely. Species of the *caesioannulata*-group are found in the northcentral Appalachians north to Pennsylvania, west to Ohio and Illinois, and south to Arkansas.

Cleidogona celerita Williams and Hefner
Figures 374–377

Cleidogona celerita Williams and Hefner, 1928, Bull. Ohio Biol. Surv., 18: 117, fig. 14c, ♂.
Cleidogona inflata Causey, 1951, J. Washington Acad. Sci., 41: 90, figs. 14–19, ♂. NEW SYNONYMY.

Types. Male holotype of *C. celerita* from "Ohio," in USNM (Type No. 2271), examined; male holotype of *C. inflata* from Starved Rock State Park, Putnam Co., Illinois, in Illinois Natural History Survey Collection, examined.

Diagnosis. The swollen appearance of the anterior gonopods (Fig. 374) differentiates this species from any other occurring in North America.

Description of male holotype. Length, 18 mm, A3 = 1.00 mm. Ocelli 28 in 6 rows. Coloration typical. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 375), sternum broad, extending between colpocoxites as a quadrate piece; coxal knobs not obvious, coxae setose, wrinkled. Colpocoxites with subapical corrugations and subapical process, colpocoxite tip divided. In lateral view (Fig. 374), colpocoxite and coxa enormously swollen posteriorly, anterior branch of colpocoxite apex rodlike, posterior branch broad, curved, laciniate on posterior surface. Telopodite small, thin. Posterior gonopods (Fig. 376): reminiscent of those of species of *mississippiana*-group, basal process cylindrical, notch absent, apical coxal process with small knobs. Coxae 10 and 11 and sternal process 12 as usual.

Description of female from Urbana, Ill. Length, 20 mm, A3 = 1.05 mm. Ocelli 29 in 6 rows plus single ocellus. Nonsexual characters as in male. Cyphopods (Fig. 377): valves not ornamented; postgenital plate low and irregular.

Distribution. Williams and Hefner (1928) report this species as "general throughout Ohio." I have not seen any Ohio specimens except the holotype. ILLINOIS: *Lake Co.*, Volvo Bog, Volvo, D. F. Reichle, 22 July 1962, ♂♂; *Champaign Co.*, Champaign, 11 July 1921, A. Weese, ♂♂♀ (MCZ); Urbana, no date or collector's name, ♂ ♀ (MCZ).

Cleidogona caesioannulata (Wood)
Figures 378–384

Spirostrephon caesioannulatus Wood, 1865, Trans. Amer. Philos. Soc., 13: 194, no figures.
Cleidogona caesioannulata, Cook and Collins, 1895, Ann. New York Acad. Sci., 9: 43–47, figs. 138, 139, 145–148, 150, ♂; Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull., 212: 90 (notes on synonymy); *not* Williams and Hefner, 1928, see *C. fustis.*
Cleidogona exaspera Williams and Hefner, 1928, Bull. Ohio Biol. Surv., 18: 117, new name for *C. caesioannulata* as described by Cook and Collins (1895). NEW SYNONYMY.

Types. Female holotype of *S. caesioannulatus* from "Western Pennsylvania," in Acad. Nat. Sci., Philadelphia (No. 11202), examined; male holotype of *C. exaspera* from Delaware Co., Ohio, in USNM (Type No. 2270), examined.

Diagnosis. Differs from the most closely related species, *C. laminata*, in the form of the coxal process of the anterior gonopods.

Description of male from Wooster, Ohio. Length, 20 mm, A3 = 0.80 mm. Ocelli 27 in 6 rows. Coloration as usual. Segments (Fig. 382) cylindrical. Anterior gonopods: in lateral view (Fig. 378), coxae broad at base, setose, with subquadrate coxal process; colpocoxites with small lateral tooth above coxal process, apex divided and bent at right angle to body of colpocoxite, posterior branch the longest. Telopodites slender basally, apically swollen, of moderate size. Posterior gonopod (Fig. 383): similar to *C. celerita* and to some members of the *mississippiana*-group. Coxae 10 and 11 and sternal process 12 as usual (Fig. 382).

Description of female from Wooster, Ohio. Length, 21 mm, A3 = 0.82 mm. Nonsexual characters as in male. Cyphopods (Fig. 384): median valves with median carinae; postgenital plate divided, with two upright arms.

Distribution. It should be noted that most of the many records of this species in the early literature apply to other, then undescribed, species. Until 1895, *caesioannulata* was thought to be the only species of its genus. See Map 12. INDIANA: *Monroe Co.*, reported by Cook and Collins (1895). NORTH CAROLINA: *Durham Co.*, Duke Forest, 6–25 November 1952, A. S. Pearse, ♂♂♀♀; *Yancey Co.*, Mt. Mitchell, 29 November 1950, N. Causey, ♂♂; Mt. Mitchell summit (6600 ft.), balsam forest, 30 October 1969, W. Shear, ♂. OHIO: *Delaware Co.*, reported by Williams and Hefner (1928); *Wayne Co.*, Highland Park, Wooster, May 1959, A. Weaver, ♂♂; Funk's Hollow, 10 May 1962, A. MacDougall, ♀. PENNSYLVANIA: *Montgomery Co.*, Bryn Mawr, October 1952, R. Stuart, ♂♂♀♀; *Monroe Co.*, Stroudsburg, 15 May 1962, F. B. Busser, ♀♀. VIRGINIA: *Alleghany Co.*, Lowmoor, 2 mi. west of Clifton Forge, 4 October 1949, R. Hoffman, ♂♂; Clifton Forge, 20 October 1956, R. Hoffman, ♂♂ ♀♀; 3 mi. northwest of Clifton Forge, 15 September 1947, R. Hoffman, ♂; *Appomattox Co.*, 1.5 mi. northeast of Vera, 5 October 1952, R. Hoffman, ♂♀; *Augusta Co.*, Elliott's knob (4470 ft.), 26 September 1949, R. Hoffman, ♂♀♀; *Bedford Co.*, Peaks of Otter, October 1960, R. Hoffman, ♂♂♀♀; *Campbell Co.*, Long Mt., 1 mi. northwest of Rustburg, 5 October 1962, L. Hubricht, ♂♂; *Giles Co.*, Mountain Lake, 2–8 August 1948, H. K. Wallace, ♂♂♀♀; *Henry Co.*, Ridgeway, 27 November 1961, R. Hoffman, ♂; *Montgomery Co.*, Roanoke River bluff, 1 mi. east of Shawsville, 22 April 1956, R. Hoffman, ♂♂♀; Blacksburg, 28 October 1956, R. Hoffman, ♂♂♀♀; *Roanoke Co.*, Poor Mt., 15 October 1956, R. Hoffman, ♂♂.

Notes. Williams and Hefner (1928) confused this species with *C. fustis*, illustrating *C. fustis* as *C. caesioannulata*, and true *C. caesioannulata* under the name *C. exaspera*, which they proposed for Cook and Collins' (1895) concept of *C. caesioannulata*. Williams and Hefner (1928) based their assumption on data from McNeill (1887), who had specimens from Indiana, and which, judging by his illustrations, were either *C. caesioannulata* or *C. laminata*. The earlier reports of Packard and Bollman are treated in Cook and Collins (1895); it is enough to say here that Packard's material from Alabama and Mississippi and Bollman's from east Tennessee are not *C. caesioannulata*.

The female holotype was said to be from Alleghany County, Pennsylvania, by Chamberlin and Hoffman (1958), but is only labelled "Western Pennsylvania." It is in poor condition, but clearly identifiable as to species by the shape of the postgenital plate (see Fig. 384). Thus Cook and Collins' (1895) prediction that *C. major* would eventually be proved a synonym of *C. caesioannulata* is rejected (compare Fig. 296). The two species are sympatric at Washington, D. C., and throughout much of Virginia.

There is some variation in the gonopods of this widespread species. Figure 379 represents a lateral view of the apical part of the anterior gonopod of a specimen from Peaks of Otter, Bedford County, Virginia; the main difference from Ohio specimens is in the form of the coxal process. Specimens from Campbell County, Virginia, conform to this figure as well. The apex of an anterior gonopod of a specimen from Mt. Mitchell, Yancey County, North Carolina, is shown in Figure 380; the distal corner of the coxal process is drawn out, and the anterior apical branch of the colpocoxite is shorter than in the Ohio material.

Specimens from Henry County, Virginia, also resemble this figure. Figure 381 shows the tip of the colpocoxite of a male from Clifton Forge, Alleghany County, Virginia; the coxal process of this specimen is as in the Ohio specimens. Specimens from Montgomery, Roanoke and Augusta counties, Virginia, are similar, but intergrade with the type of colpocoxite apex seen in Figure 379.

Cleidogona laminata Cook and Collins
Figures 385–387

Cleidogona laminata Cook and Collins, 1895, Ann. New York Acad. Sci., 9: 48, figs. 164–171, ♂.
Cleidogona aspera Causey, 1951, J. Washington Acad. Sci., 41: 78, figs. 1–4, ♂. NEW SYNONYMY.

Types. Male holotype of *C. laminata* "probably from Indiana (Cook and Collins, 1895)" but probably not, see below, in USNM (No. 427), examined; male holotype and female paratype of *C. aspera* from 6 mi. east of Imboden, Lawrence Co., Arkansas, deposited in Philadelphia Academy of Sciences, but subsequently lost in mail.

Diagnosis. Very close to *C. caesioannulata*, but distinct in not having the apex of the gonopod colpocoxites turned over at right angles to the body of the gonopod (Fig. 386, compare Fig. 378).

Description of male from Pocahontas, Arkansas. Length, 19 mm, A3 = 0.90 mm. Ocelli 29 in 7 rows. Coloration typical. Segments cylindrical. Anterior gonopods: as in Figures 385, 386, almost identical to those of *C. caesioannulata;* apex of colpocoxite not bent, posterior branch with 2 small terminal branches. Posterior gonopod (Fig. 387) more closely resembles those of species of the *mississippiana*-group than does that of *C. caesioannulata,* differing from that species in the lesser expansion of the second segment. Coxae 10 and 11 and sternal process 12 all as in *C. caesioannulata.*

Females have been collected, but none were available for this study.

Distribution. ARKANSAS: *Clay Co.,* Pocahontas, 22 March 1950, N. Causey, ♂; reported by Causey (1951a) from *Randolph Co.,* Pocahontas, and from *Dallas Co.,* Carthage. LOUISIANA: *Jackson Par.,* 7 mi. east of Ruston, 29 October 1954, W. Stevens, ♂.

Notes. The male holotype of Cook and Collins' species was unlabelled, but as it probably came from the Bollman collection, they assumed that it had been collected in Indiana, where Bollman did most of his work. However, it seems now that it is much more likely that the specimen originated in Arkansas, a region from which Bollman also received material from time to time. I compared the holotype of *C. laminata* with specimens of *C. aspera* labelled as such by Causey and found no differences; thus as first reviser, I designate the type locality of *C. aspera* (6 mi. east of Imboden, Lawrence Co., Arkansas) as the type locality of *C. laminata.*

This species represents a southern offshoot of the *C. caesioannulata* stock, and clearly connects the *caesioannulata*-group with the *mississippiana*-group.

THE *UNITA* GROUP

This group is probably derived from the *major*-group, but at the same time resembles species of *Tiganogona* in the simplicity of the anterior gonopods. Besides the species discussed in detail below, *C. arkansana* and *C. minima* Causey (see section on species not included in revision) also belong to this group. Species of the *unita*-group occur in the Midwest from Illinois and Kentucky to Arkansas and Alabama.

Cleidogona unita Causey
Figures 388–393

Cleidogona unita Causey, 1951, J. Washington Acad. Sci., 41: 78, figs. 5–9, ♂.

Types. Male holotype and female paratypes from Giant City State Park, Union

Co., Illinois, deposited in collection of Illinois Natural History Survey, examined.

Diagnosis. Distinguished from *C. accretis* (Fig. 395) in the narrower colpocoxites of the anterior gonopod in lateral view (Fig. 389). This species cannot profitably be compared to *C. arkansana* and *C. minima* in the absence of specimens of those species.

Description of male holotype. Length, 15 mm, A3 = 0.60 mm. Ocelli 26 in 5 rows plus single ocellus. Coloration typical. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 388), sternum broadly triangular between colpocoxites, coxal knobs rather small; colpocoxites short and curved, not divided. In lateral view (Fig. 389), coxa without process, colpocoxite basally broad, distal part set off by distinct notch, distal part bladelike, with few broad ridges on anterior ventral surface. Telopodites rodlike, S-shaped. Posterior gonopods (Fig. 391): details reduced from *C. caesioannulata* type; broadest part of second segment just beyond midlength. Coxae 10 and 11 and sternal process 12 as usual for genus.

Description of female paratype. Length, 15.5 mm, A3 = 0.62 mm. Nonsexual characters as in male. Cyphopods (Fig. 393): valves with processes and laminae; postgenital plate (Fig. 392) not divided, margin regular.

Distribution. In addition to the type locality, the following: ILLINOIS: *Jackson Co.*, Grand Tower, Pine Hills, off Rt. 3, 23 October 1966, F. Schmidt, ♂; *Union Co.*, Pine Hills, 23 October 1926, J. Beatty, ♂; 8 mi. south-southwest of Carbondale, 22 October 1966, J. M. Nelson, ♂; reported by Causey (1951) from *Pope Co.*, Dixon Springs. KENTUCKY: *Edmonson Co.*, Mammoth Cave Hollow, Mammoth Cave National Park, 25 November 1960, D. Reichle, ♂.

Notes. The apex of the anterior gonopods of specimen from Mammoth Cave National Park, Kentucky, is shown in Figure 390.

Cleidogona accretis n. sp.

Figures 394–396

Types. Male holotype and other males from 2 mi. southwest of Increase, near Little Creek, Lauderdale Co., Mississippi, collected by L. Hubricht, 3 December 1961. The species name refers to the type locality.

Diagnosis. Distinct from *C. unita* (Fig. 389) in the shorter colpocoxites of the anterior gonopods (Fig. 395).

Description of male holotype. Length, 9.5 mm, A3 = 0.54 mm. Ocelli 26 in 5 rows. Coloration pale, but typical. Segments cylindrical. Anterior gonopods: in anterior view (Fig. 394), colpocoxites well separated by sternum, sternum with longitudinal fovea in midline, oblique wrinkles; coxal knobs prominent. In lateral view (Fig. 395), coxa with blunt process near apical part; colpocoxite short, hoodlike; telopodites rodlike, evenly curved. Posterior gonopods (Fig. 396): somewhat reduced, coxae without processes; second segment not much enlarged. Coxae 10 and 11 and sternal process 12 as usual for genus.

Female unknown.

Distribution. Known only from the type locality.

THE *FUSTIS* GROUP

Cleidogona fustis Cook and Collins

Figures 397–400

Cleidogona fustis Cook and Collins, 1895, Ann. New York Acad. Sci., 9: 49, figs. 151–153, ♂.

Cleidogona caesioannulata, Williams and Hefner, 1928, Bull. Ohio Biol. Surv., 18: 116, fig. 14A, ♂; not *C. caesioannulata* (Wood), 1865, or Cook and Collins, 1895; see discussion in *Notes* under *C. caesioannulata.*

Types. Male holotype from "Indiana," deposited in USNM (No. 446), not examined, presumed lost. Number 446 is not a diplopod, according to the curator (R. Crabill, in litt.).

Diagnosis. The thin colpocoxites of the anterior gonopods, with two subequal apical branches turned anteriad (Fig. 398), distinguish this species from all others.

Description of male from Athens, West Virginia. Length, 16 mm, A3 = 0.60 mm. Ocelli 27 in 6 rows. Coloration typical. Segments cylindrical. Anterior gonopods: in posterior view (Fig. 397), telopodites thin, rodlike, fused at base; anterior colpocoxite branch broadly lamellate, transparent, posterior branch rodlike, posterior faces finely laciniate. In lateral view (Fig. 398), coxa without process, apical divisions of colpocoxite turned anteriad; telopodites with small subterminal teeth. Posterior gonopod (Fig. 399): resembling *C. caesioannulata.* Coxae 10 and 11 and sternum 12 as usual.

Description of female from Athens, West Virginia. Length, 16 mm, A3 = 0.65 mm. Nonsexual characters as in male. Cyphopods: valves (Fig. 400) with long posterior rodlike lamellae; postgenital plate nearly diamond-shaped, similar to those of species of *alata*-group.

Distribution. Indiana: *Montgomery Co.,* reported by Chamberlin and Hoffman (1958); *Jefferson Co.,* Clifty Falls State Park, near Madison, reported by Williams and Hefner (1928). Kentucky: *Carter Co.,* 3 mi. east of Grayson, 19 April 1961, R. L. Hoffman, ♂. Virginia: *Montgomery Co.,* 5 mi. northeast of Blacksburg, R. Hoffman and W. Shear, 10 April 1969, ♂; *Pulaski Co.,* Draper Mt. above Pulaski, 4 October 1959, R. Hoffman, ♂; *Russell Co.,* 1 mi. north of Lynn Spring, 20 April 1962, R. Hoffman, ♂; *Tazewell Co.,* Burkes Garden, top of Clinch Mt., 14 November 1965, Radford College Biology Club, ♂. West Virginia: *Fayette Co.,* Babcock State Park, 2 April 1967, W. Shear, ♂♀; *McDowell Co.,* Kimball, 19 May 1966, S. Romeo, ♂; *Mercer Co.,* Athens, 22 October 1966, W. Shear, 30 March 1967, R. Wertheim, 23 March 1968, N. Price, ♂♂♀♀; 2 mi. south of Athens on Rt. 20, 16 October 1966, W. Shear, ♂; Camp Creek State Forest, 20 February 1966, 26 March 1967, W. Shear, ♂♂♀; Brush Creek Falls, 10 November 1966, L. Bayless, ♂; *Raleigh Co.,* Grandview State Park, 6 May 1967, W. Shear, ♀; 5 mi. east of Shady Spring, 14 December 1965, R. Hoffman, ♂♂♀♀; *Summers Co.,* Bluestone State Park, 27 March 1968, W. Shear, ♀♀; Bull Falls Recreation Area (Bluestone Reservoir), 7 April 1967, W. Shear, ♂♀; 4.2 mi. southeast of Bellepoint, 12 December 1965, R. Hoffman, ♀♀.

Notes. See notes section under *C. caesioannulata* for an explanation of Williams and Hefner's (1928) confusion between *C. fustis* and that species. *Cleidogona fustis* is related to the *major*- and *caesioannulata*-groups.

Genus *Tiganogona* Chamberlin

Bactropus Cook and Collins, 1895, Ann. New York Acad. Sci., 9: 53. Preoccupied by *Bactropus* Barrande, 1872, fossil Crustacea.

Tiganogona Chamberlin, 1928, Entomol. News, 39: 154; Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull., 212: 96–97 (list of species).

Ofcookogona Causey, 1951, Proc. Biol. Soc. Washington, 64: 120; Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull., 212: 93 (list of species). NEW SUBJECTIVE SYNONYMY.

Ozarkogona Causey, 1951, J. Washington Acad. Sci., 41: 82; Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull., 212: 93 (list of species). NEW SUBJECTIVE SYNONYMY.

Bactropodellus Jeekel, 1969, Entomol. Bericht., 29: 88 (new name to replace *Bactropus* Cook and Collins). NEW SUBJECTIVE SYNONYMY.

Type species. Of *Bactropus* and *Bactropodellus, B. conifer* Cook and Collins, by monotypy; of *Tiganogona, T. brownae* Chamberlin, by original designation; of *Ofcookogona, O. steuartae* Causey, by original designation; of *Ozarkogona, O. glebosa* Causey, by original designation.

Notes on synonymy. The unique holotype of *Bactropus conifer,* type species of *Bactropodellus* (*Bactropus*) has been lost, but the illustrations presented by Cook and Collins (1895, figs. 172–176) leave no doubt that *B. conifer* is congeneric with *Tiganogona brownae.* In particular, the high shoulders of the lateral sternal sclerites, the simple anterior gonopod colpocoxites and the form of the posterior gonopods place *B. conifer* here. The distinguishing characters of *Ofcookogona* and *Ozarkogona* are minor differences in the lobation of coxae of the posterior gonopods and the number of telopodite segments. These differences are hardly of species importance.

Jeekel (1969) first pointed out that the generic name *Bactropus* was preoccupied, but did not attempt to determine if any other names might be available for the genus. Thus he proposed the new name *Bactropodellus*. The gender of the name *Tiganogona* is believed to be feminine.

Diagnosis. Distinct from *Pseudotremia* and *Solaenogona* in lacking a colpocoxite branch bearing a gland channel; from *Dybasia* in having the sternite of the anterior gonopods completely fused to the coxae; and from *Cleidogona* in the simplicity of the anterior gonopods and the form of the posterior gonopod coxae.

Description. Thirty segments. Mentum divided (Fig. 181). Antennae long, article 3 the longest. Ocelli always present. Body fusiform, widest in males at segment 7, tapering evenly posteriad. Body segments more or less cylindrical, surface of segments smooth, sides of segments without prominent lateral striations. Pregonopodal legs of males: as described for *Cleidogona*. Anterior gonopods: basic construction as in *Cleidogona*, but lateral sternal sclerite usually much larger, with high angular shoulders (Fig. 401). Coxae and colpocoxites more solidly fused than usual in *Cleidogona*; coxal region with setae, colpocoxite region usually simple and bladelike. Telopodites simple. Posterior gonopods: coxae bearing series of complex lobes (Fig. 413), or with a single curved lobe (Fig. 402); *in situ*, telopodites of anterior gonopods locking around lobes (Fig. 407). Telopodites much reduced, 3-segmented to 1-segmented (Figs. 402, 408, 411, 413). Postgonopodal legs: coxa 10 with gland sessile (Fig. 403), large rugose apical knob. Coxa 11 with gland sessile, not modified; prefemur 11 with mesal plate about midlength (Fig. 404). Sternum 12 not modified. Female cyphopods: postgenital plate usually absent, see Figures 405, 409, 414.

Distribution. See Map 10, open symbols. Indiana, Missouri, Arkansas, and Louisiana.

Identifications. Half of the species assigned to this genus are known only from unique type specimens that could not be located; thus it seems futile to present a key to the remaining half of the genus, discussed species by species below.

Tiganogona brownae Chamberlin
Figures 401–405

Tiganogona brownae Chamberlin, 1928, Entomol. News, 39: 154; Causey, 1951, Proc. Biol. Soc. Washington, 64: 124, figs. 17, 18, ♂.

Types. Male holotype and female paratype from St. Charles, St. Louis Co., Missouri, in University of Utah collection, examined.

Diagnosis. Closest to *T. moesta* and *T. alia;* differs from *T. moesta* in the larger anterior gonopod telopodites (compare Figs. 401 and 406) and from *T. alia* in the 2-segmented posterior gonopod telopodites (Fig. 402).

Description of male holotype. Length, 12 mm, A3 = 0.54 mm. Ocelli 28 in 6 rows. Coloration typical, as in species of *Cleidogona*. Segments cylindrical. Anterior gonopods: in lateral view (Fig. 401), lateral sternal sclerite triangular, well set off. Colpocoxite simple, bladelike, apex with three teeth. Telopodite long, as long as colpocoxite, rodlike, with distal hook. Blunt process from base of colpocoxites. Posterior gonopods: sternum broad, not well sclerotized (Fig. 402), with large median knob rugose. Gonopod coxae elongated mesally to form lobe as long as rest of gonopod; telopodites with two segments and claw, first telopodite segment cylindrical, second globose. Coxae 10 and 11 (Figs. 403, 404) as described for genus.

Description of female paratype. Length, 12 mm, A3 = 0.52 mm. Ocelli *ca.* 27, head crushed. Nonsexual characters as in male.

Cyphopods (Fig. 405) with median valve high, knobby; postgenital plate absent, but coxae 2 much extended ventrolaterally.

Distribution. Known definitely only from type locality, but reported by Causey (in litt.) from "most of Missouri."

Tiganogona moesta Causey
Figures 406–409

Tiganogona moesta Causey, 1951, J. Washington Acad. Sci., 41: 82, figs. 22, 23, ♂.

Types. Male holotype from Blue Spring, Carroll Co., Arkansas, in Philadelphia Academy of Sciences, apparently lost in mails, not seen.

Diagnosis. Distinct from *T. brownae* in the characters given under that species. The anterior gonopods (Fig. 406) resemble those of *T. stewartae*, as illustrated by Causey (1951a, fig. 13), but apparently differ in having teeth on the apical part of the colpocoxites.

Description of male from Cave Creek Valley, Arkansas. Length, about 12 mm, A3 = 0.57 mm. Ocelli 27–28 in 6 rows. Coloration typical. Segments cylindrical. Anterior gonopods: in lateral view (Fig. 406), lateral sternal sclerite squared off, anterior sternal sclerite with triangular lateral projection. Coxal area with only 2 setae; colpocoxite as in *T. brownae*, but with more apical posterior teeth. Telopodite much shorter than colpocoxite, rodlike, slightly curved, pointed at tip. Posterior gonopods (Fig. 408): as in *T. brownae*, but telopodites 3-segmented, apical segment small, cylindrical. Coxae 10 and 11 as described for *T. brownae*.

Description of female from Cave Creek Valley, Arkansas. Length, about 12–15 mm, A3 = 0.54 mm. Nonsexual characters as in male. Cyphopods much like those of *T. brownae;* mesal valves somewhat larger (Fig. 409).

Distribution. In addition to the type locality: ARKANSAS: *Washington Co.*, Cave (Cove?) Creek Valley, 10 November 1955, collector's name illegible, ♂♀.

Tiganogona alia (Causey) NEW COMBINATION
Figures 410, 411

Ofcookogona alia Causey, 1951, Proc. Biol. Soc. Washington, 64: 121, figs. 14–16, ♂.

Types. Male holotype from Junction City, Union Co., Arkansas, in Philadelphia Academy of Sciences, evidently lost in mails, not seen.

Diagnosis. Distinct from the other species illustrated here in the single-segmented posterior gonopod telopodite (Fig. 411), which is short and globose, rather than elongate and clavate as in *T. glebosa* (Fig. 413).

Description of male from Ruston, Lincoln Co., Louisiana. Length, about 12 mm, A3 = 0.53 mm. Ocelli 24–25 in 5 rows. Coloration typical. Segments cylindrical. Anterior gonopods: in lateral view (Fig. 410), with lateral sternal sclerite extending far posteriad, triangular in shape, covering bases of coxal setae. Colpocoxites simple, somewhat flattened anteroposteriorly, with large blunt, curved process at base; telopodites small, simple, curved, acuminate. Posterior gonopods (Fig. 411): sternum poorly sclerotized, with long, thin knob on midline, laterally cupping posterior gonopod coxae; coxae large, lobed as in Figure 411; telopodite a single globular segment with small, reduced claw. Coxae 10 and 11 as described for *T. brownae*.

Female unknown.

Distribution. In addition to the type locality: ARKANSAS: *Washington Co.*, December 1958, G. Ogden, ♂♂. LOUISIANA: *Lincoln Co.*, Ruston, 18 March 1955, W. J. Harman, ♂♂.

Tiganogona glebosa (Causey) NEW COMBINATION
Figures 412–414

Ozarkogona glebosa Causey, 1951, J. Washington Acad. Sci., 41: 82, figs. 20, 21, ♂.

Types. Male holotype from Fayetteville, Washington Co., Arkansas, in Philadelphia Academy of Natural Sciences, evidently lost in mails, not seen.

Diagnosis. See diagnosis of *T. alia.*

Description of male from Clear Creek, Washington Co., Arkansas. Length, 14 mm, A3 = 0.63 mm. Ocelli 28 in 6 rows. Coloration typical. Segments cylindrical. Anterior gonopods: in lateral view (Fig. 412) with lateral sternal sclerite smaller than other members of genus illustrated here, not extending posteriad of coxae. Coxal portion heavily setose; colpocoxite simple, sharply curved near tip to form a hook. Telopodite nearly as large as colpocoxite, bulky, much enlarged apically, slightly curved anteriad. Posterior gonopods (Fig. 413): sternum weak, median sternal knob much reduced. Coxae large, swollen, complexly lobed as shown; telopodite single-segmented, as long as coxae, clubshaped, 1 or 2 vaguely indicated sutures near distal end; claw pointed, but small. Coxae 10 and 11 as described for *T. brownae.*

Description of female from Clear Creek, Washington Co., Arkansas. Length, 15 mm, A3 = 0.65 mm. Nonsexual characters as in male. Cyphopods as in Figure 414.

Distribution. In addition to the type locality: Arkansas: *Washington Co.*, Clear Creek, 14 February 1955, J. Hastings, ♂♂ ♀♀.

Genus *Dybasia* Loomis

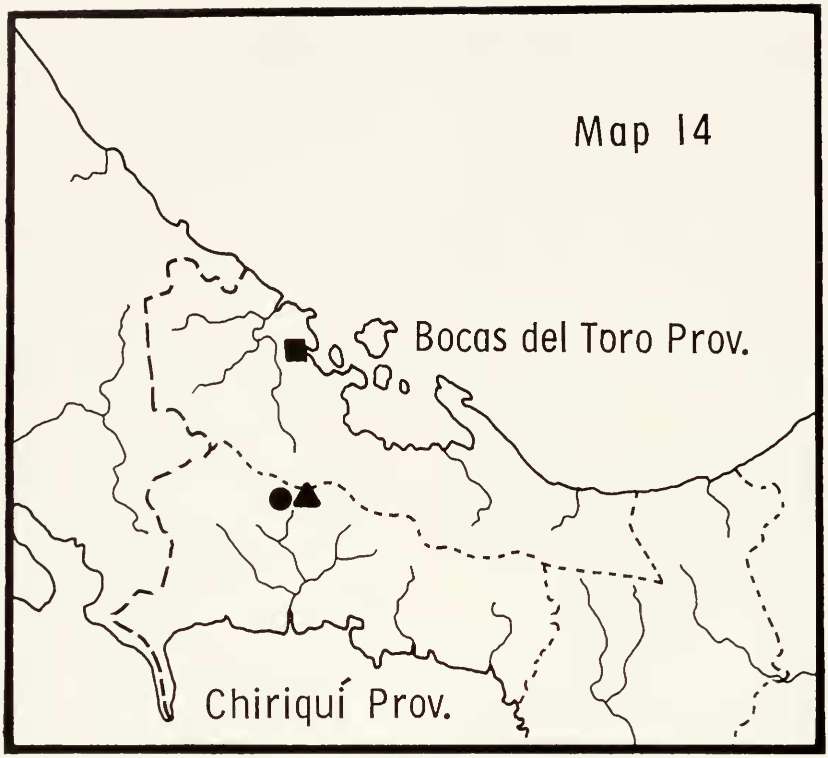
Dybasia Loomis, 1964, Fieldiana, 47: 100.
Ogkomus Loomis, 1964, Fieldiana, 47: 102. NEW SUBJECTIVE SYNONYMY.
Solemia Loomis, 1964, Fieldiana, 47: 104. NEW SUBJECTIVE SYNONYMY.

Types. Of *Dybasia, D. humerosa* Loomis; of *Ogkomus, O. divergens* Loomis; of *Solemia, S. chiriquia* Loomis; all by monotypy and original designation. The gender of the generic name is feminine.

Notes on synonymy. The three monotypic genera combined here in *Dybasia* were proposed by Loomis (1964) in the same paper. As first reviser, I select *Dybasia* as the generic name. Though Loomis considered these species as constituting a distinct family (Dybasiidae) related to the cleidogonids, an examination of the specimens has convinced me that such a placement is at this time unjustified; indeed it may eventually prove necessary to include these species in *Cleidogona.* Unfortunately, the similarity between *Dybasia divergens* and *Cleidogona minutissima* could not be explored because of a lack of material. For the time being I prefer to recognize the genus on the basis of the peculiarities of the sternum of the anterior gonopods, the segmental paranota, the form of the posterior gonopods, and their zoogeographic distinctness, all characters which mark the species in *Dybasia* as a uniform group. The other characters given by Loomis (1964) as diagnostic for the family Dybasiidae and the three genera included in it are to be found in numerous species of *Cleidogona.* In particular, his statement that the anterior gonopod sternum is "very small or lacking" in the Cleidogonidae is obviously in error.

Diagnosis. Closely related to *Cleidogona,* but differing primarily in the sternum of the anterior gonopods, which in *Dybasia* is free from the anterior median faces of the coxae and drawn out ventrad into a pair of more or less prominent processes, longest in *D. humerosa,* but much shorter in *D. divergens.*

Description. Thirty segments. Mentum divided. Antennae of moderate length, shorter than in *Cleidogona* and *Pseudotremia.* Ocelli always present. Body fusiform, most body segments with prominent paranota, somewhat resembling members of the family Conotylidae. Surface of segments smooth. Segmental setae prominent, never spatulate. Sides of segments without lateral striations. Pregonopodal legs of males: as described for *Cleidogona.* Anterior gonopods: sternum broad, well sclerotized, not fused firmly to gonopod coxae, bearing pair of anterior processes. Lateral sternal sclerite distinct. Coxae large, irregular, setae sometimes lacking. Colpocoxites simple, with large angular shoulders at coxal junction, evenly curved, usually cupped posteriad. Telopodites re-



Map 14. Northern Panama, showing distribution of the genus *Dybasia*. Dot, *D. humerosa*; triangle, *D. chiriquia*; square, *D. divergens*.

duced, nearly absent in some species. Posterior gonopods: 4-segmented, coxae variously modified. Tenth and eleventh coxae and twelfth sternum as described for *Cleidogona*. Female cyphopods: valves keeled, postgenital plate absent.

Distribution. Northern Panama. See Map 14.

Key to Males of Species of *Dybasia*

1a. Sternal processes of anterior gonopods short, diverging, not meeting in midline (Fig. 419) .... *divergens*
1b. Sternal processes of male gonopods more or less elongate, meeting in midline (Figs. 416, 423) 2
2a. Coxae of posterior gonopods of male shorter than second segment, with single process (Fig. 424) .... *chiriquia*
2b. Coxae of posterior gonopods of male longer than second segment, with two processes (Fig. 415) .... *humerosa*

Dybasia humerosa Loomis
Figures 415–418, Map 14

Dybasia humerosa Loomis, 1964, Fieldiana, 47: 101, figs. 10A–I, ♂.

Types. Male holotype from "Casita Alta," Finca Lerida, near Boquete, Chiriquí Province, Panama, collected 18 March 1959 by H. S. Dybas, deposited in Field Museum of Natural History, examined. The specific name probably refers to the shoulders on each segment.

Diagnosis. As in the above key.

Description of male holotype. Length, 10 mm, A3 = 0.50 mm. Ocelli 23 on left side, 25 on right side, in subtriangular patch. Coloration typical of *Cleidogona*, midbody segments with raised shoulders, but dorsum not flat, shoulders about one-fourth body width, body segments beyond

23–24 cylindrical. Anterior gonopods: in anterior view (Fig. 416), sternum broad, well sclerotized; sternal processes translucent, joined basally at midline, somewhat enlarged apically, anterior apical face of each process rugose. Coxae with high, thick shoulders; basal knob projecting anteriad. Colpocoxites thin, cupped posteriad, lateral margin (Fig. 417) sinuate. Telopodites nearly obsolete, fused into small knob at posterior coxal bases. Posterior gonopods: 5-segmented. Coxae largest and longest segments, with blunt basal processes, more acute midapical processes rugose and set with stiff setae. Second segments cylindrical, apical 3 segments reduced in size (Fig. 415). Coxae of legs 10 and 11 with gland petiolate, each with prominent mesal knob above gland opening. Sternum 12 with long typical process as in *Cleidogona*, reaching to sternum 10.

Description of female paratype. Length, 11 mm, A3 = 0.52 mm. Nonsexual characters as in male, but segmental shoulders not so prominent on anterior segments. Cyphopods (Fig. 418) with completely fused, keeled valves. Postgenital plate absent.

Distribution (from Loomis, 1964). PANAMA. *Chiriquí Province*, "Casita Alta," Finca Lerida, near Boquete, from forest floor litter, 5650 ft., 6900 ft., 7750 ft., 7800 ft., 14–18 March 1949, H. Dybas; Cerro Punta, 6900 ft., 7 March 1959, H. Dybas. All of these records are based on females and immature specimens. *Dybasia humerosa* is syntopic or nearly so with *D. chiriquia* at Finca Lerida, and I am unable to distinguish females and young of the two species. None of the females of *D. chiriquia* reported by Loomis (1964) are mature.

Notes. Loomis shows the posterior gonopod (Loomis, 1964: 103, fig. 10–H) with the coxa divided into two segments and the apical three reduced to two. In Loomis' figure 10–I, the sternal processes of the anterior gonopods are shown as fused nearly up to their distal ends.

Dybasia divergens (Loomis)
NEW COMBINATION
Figures 419–421, Map 13

Ogkomus divergens Loomis, 1964, Fieldiana, 47: 102; figs. 10J–L.

Types. Male holotype and three female paratypes from Almirante, Bocas del Toro Province, Panama, collected from forest floor litter by H. S. Dybas, 1 April 1959, deposited in Field Museum of Natural History, examined. The specific name probably refers to the diverging sternal processes.

Diagnosis. Distinct from the other two species of the genus in the details of the gonopods, and the characters given in the above key.

Description of male holotype. Length, 11.5 mm, A3 = 0.55 mm. Ocelli 26 on both sides of head. Coloration typical. Segments similar to those of *D. humerosa*, shoulders somewhat less pronounced. Anterior gonopods: sternum (Fig. 419) broad, well sclerotized, slightly depressed at base of sternal processes; sternal processes short, diverging. Coxae and lateral sternal sclerites with pronounced shoulders. Colpocoxites right-angled in lateral view (Fig. 420), with apical lateral hooklike process. Telopodites small, knoblike, fused basally but distinct distally. Posterior gonopods (Fig. 421): intermediate between those of *D. humerosa* and *D. chiriquia;* coxae and second segments subequal in length, coxae with proximal and distal lobes. Tenth and eleventh legs with coxae essentially unmodified. Twelfth sternum as described for *D. humerosa*, but process shorter.

Mature females that can be assigned with certainty to this species have not been collected.

Distribution. Known only from the type locality.

Notes. I did not see the basal pore in coxa of the posterior gonopod illustrated by Loomis (1964: 103, fig. 10–L). None of the females from the type locality (designated by Loomis as paratypes) are mature.

Dybasia chiriquia (Loomis)
NEW COMBINATION
Figures 422–424, Map 13

Solemia chiriquia Loomis, 1964, Fieldiana, 47: 105; figs. 10M–P, ♂.

Types. Male holotype from Finca Lerida, near Boquete, Chiriquí Province, Panama, elev. 5600 ft., collected 12 March 1959 by H. S. Dybas, female and juvenile paratypes from same locality, deposited in Field Museum of Natural History, examined. The specific name refers to Chiriquí Province.

Diagnosis. Distinct in the details of the gonopods, and the characters given in the key.

Description of male holotype. Length, 12 mm, A3 = 0.55 mm. Ocelli 26 on left side of head, 27 on right side. Coloration typical. Segments as in *D. humerosa.* Anterior gonopods: sternum (Fig. 422) low, more poorly sclerotized than in preceding 2 species; sternal processes thin but broad, abruptly diverging, anterior faces slightly rugose. Coxae with shoulders less prominent than in *D. humerosa.* Colpocoxites (Fig. 423) broad, cupped, resembling *D. humerosa,* but edges not sinuate; posterior margin with small subapical hook. Telopodites largest in genus, distinctly separate, recurved. Posterior gonopods (Fig. 424): coxae shorter than second segments, bearing long knobs basally. Second segments and apical 3 segments typical.

Females that can be assigned to this species with certainty have not been collected. See *Notes* below.

Distribution. Known only from the type locality. A few females and young collected by G. A. Solem, 7 March 1959, at 6700 ft. and 7000 ft. on Cerro Punto, Chiriquí Province, Panama, have been assigned to *D. chiriquia* by Loomis (1964).

Notes. I cannot, with certainty, distinguish between females of this species and the syntopic *D. humerosa.* For this reason, I hesitate to assign the specimen to one or the other of the species, and have arbitrarily described the females under *D. humerosa.*

Part II. A Reclassification of the Order Chordeumida in the New World

INTRODUCTION

In an excellent discussion of the zoogeography of North American millipeds, Hoffman (1969a) was unable to include the Order Chordeumida because of the chaotic state of its taxonomy. An investigation of the literature reveals that little or no revisionary work has been done on this order in America since 1895. Even the most recently published papers concern themselves with either describing new species in poorly defined genera and families, thus perpetuating past errors, or with setting up superfluous new higher categories. Some of these new genera and families were based on a few specimens of single species, or, worse, on misleading literature, the author of the new name never having seen actual specimens.

In the course of revising the Family Cleidogonidae, the largest and commonest North American chordeumid family, I had occasion to examine type specimens or newly collected material of all but one North American chordeumid family, and the great majority of genera and species. Some of these observations have already been reported in the form of a revision of the family Conotylidae (Shear, 1971a) and a synopsis of the genera of North American cave millipeds, most of which are chordeumids (Shear, 1969).

It soon became apparent that the North American families I consider valid fall into four large, seemingly natural groups. Since three of these groups are exclusively North American (the third has some Asian, Australian, and South American members), I feel that no damage is done to the stability of nomenclature by recognizing them as superfamilies. Past efforts at subdividing the North American members of the Chordeumida have failed (see historical review below), usually because the taxonomists involved failed to examine specimens; thus only one of the superfamilies proposed below takes an earlier name from the superfamily level.

Following the historical review and discussion of useful characters, I present some artificial keys to the superfamilies and the included families.

Families Not Included[1]

The family Ergethidae Chamberlin, 1947, is not included here, since I have shown it to be a polydesmid rather than a chordeumid (Shear, 1971b). The family Apterouridae Loomis, 1966, cannot be treated in detail because the unique types of the only species, *Apterourus horizontalis* Loomis, have been lost. They were to have been deposited in the USNM, which has no record of having received them. This family can be treated in detail if the types are found, or if new material is collected.

---

[1] Following completion of this paper, and while it was in press, I became aware of two papers making important changes in the arrangement of families and genera in the Chordeumida:

Loomis, H. F., and R. Schmitt. 1971. The ecology, distribution, and taxonomy of the millipeds of Montana west of the continental divide. Northwest Sci., 45: 107–131.

Causey, N. B. 1969. New trichopetalid (Chordeumidea: Chordeumida) millipeds from caves in North and Central America. Louisiana Acad. Sci., 32: 43–49.

In the first, Loomis and Schmitt (1971) describe several new species and genera, as well as a new family of chordeumids from Montana. Several of these names are synonyms of older, well-established ones (i. e., *Brunsonia complexipes* Loomis and Schmitt = *Conotyla albertana* Chamberlin, etc.). Some of the species are described in the wrong families. The new family Macromastidae Loomis and Schmitt appears to be valid at this time, but I have not yet examined specimens.

Causey (1969) describes the new genus *Poterpes*, which is an obvious synonym of *Mexiterpes*. The two species *P. egeo* and *P. fishi* are closely related to *Mexiterpes metallicus,* described as new below. *Flagellopetalum appropinquo* is described, but no comparison with *F. quadratum* Loomis, from a nearby locality, is made, and *F. appropinquo* may be a synonym of *F. quadratum*.

THE HISTORY OF CHORDEUMID STUDIES

The history of the study of North American diplopods is brief, and has been summarized by Underwood (1893) and Chamberlin and Hoffman (1958). In the following review I emphasize the study of chordeumid millipeds in North America.

In 1805, Latreille first recognized the millipeds and centipeds as distinct from the Insecta, and set them apart in his "Legion" Myriapoda. Later, in 1814, Leach called this group the Class Myriapoda, encompassing the same animals. There followed, from 1833 to 1872, a progressive subdivision of this class as the complexity and heterogeneity of Latreille's and Leach's original concepts became obvious. These changes are summarized in Chamberlin and Hoffman (1958). Chamberlin and Hoffman finally established ordinal names in the Diplopoda in an authoritative manner. Their system has gained almost universal acceptance.

Though Palisot de Beauvois (1805) had described *Julus americae-borealis* (the animal now called *Narceus americanus*), the first American naturalist to describe several millipeds in a recognizable way was the eccentric C. S. Rafinesque (1820). His work was long neglected, but in 1953, Hoffman and Crabill indicated that they could recognize Rafinesque's names and reestablished three of his milliped generic names: *Narceus* (Spirobolidae), *Abacion* (Schizopetalidae) and *Pleuroloma* (Xystodesmidae). These names have been adopted and are now in general use for some of our commonest millipeds. Rafinesque apparently described no chordeumids.

In 1821, only a year after Rafinesque's *Annals of Nature*, Thomas Say published an account of the "Myriapodae" of the United States, but mentioned no chordeumids. H. C. Wood summarized his own findings on the fauna of the eastern United States in 1865, describing *Spirostrephon caesioannulatus* (now called *Cleidogona caesioannulata*), the first North American member of the Chordeumida to be described. E. D. Cope described a second species, *Pseudotremia cavernarum*, in 1869. In the years immediately following several authors described species of chordeumids, many of which have remained unrecognizable.

The real foundation for systematic studies in North American millipeds was laid by C. H. Bollman, who, before his death in 1889 at the age of 21, published 14 papers (11 more appeared posthumously) on the rich Appalachian fauna. A collection of Bollman's papers, including 11 previously unpublished ones, appeared in 1893, under the editorship of Underwood. This important work contained a catalog (p. 117) giving Bollman's summary of the American fauna. It contains 15 species of chordeumids, all under the family Craspedosomatidae (a group apparently equivalent to the present Order Chordeumida). Five genera were listed.

The next significant contribution on North American chordeumids appeared in 1895 — Cook and Collins' "Craspedosomatidae of North America," which set a standard of excellence in descriptions that has not yet been surpassed. They followed their European contemporaries in using genitalic characters and in presenting profuse illustrations of surprising accuracy. Cook and Collins took a conservative view of generic names, with the result that all 10 genera they recognized are still valid. Included were 25 species.

O. F. Cook, by training a botanist and palm specialist, established his peculiar and short-lived journal *Brandtia* in 1895. It lasted for only two years, and published Cook's own articles on Diplopoda and other arthropods. In "On recent diplopod names," Cook (1895) divided his Order

---

In any case, Causey's illustrations greatly strengthen the case for making both *Flagellopetalum* and *Zygonopus* synonyms of *Trichopetalum*.

I will treat this and other material in more detail in a forthcoming supplement to the present paper.

Coelochaeta into three suborders, the Lysiopetaloidea, Chordeumatoidea, and Striarioidea. The 10 genera and 25 species listed earlier that year in Cook and Collins (1895) were distributed in four families.

In 1910, K. W. Verhoeff began a lamentable practice of European diplopod taxonomists, that of ignoring Cook's work and attempting to place North American species in his own taxonomic system without examining specimens. As a result he duplicated some of Cook's family names, and placed other species in unrelated European families. American diplopod taxonomists either were not aware of or ignored much of Verhoeff's work. In 1932, for example, Verhoeff set up the family Trichopetalidae for *Trichopetalum,* and this was not noticed in the United States until 29 years later (Hoffman, 1961). Since Cook and Collins' paper, no revisionary work has been done on the Order Chordeumida in North America, with the result that when Chamberlin and Hoffman (1958) compiled their checklist of the United States fauna, they could list more than 100 species in 31 genera and 9 families. Five of these families contained only a single genus each and 16 of the 31 genera were monotypic. Since 1958, Verhoeff's name Trichopetalidae has been rediscovered, and three more families have been described, two of which are based on single species. The only recent extensive reworking of chordeumid higher classification has been the posthumous publication of a re-arrangement of the world fauna by Attems (1959). This classification is so absurd with regard to the North American species and in its disregard for the rules of priority that it merits no further consideration here. The reader is referred to Chamberlin and Hoffman (1958) for a summary of their classification. The three post-1958 families are added to Chamberlin and Hoffman's key by Buckett and Gardner (1967). Only one other change in the 1958 system has been made up to the present time; I have shown (Shear, 1971b) that *Ergethus perditus* Chamberlin, on which the family Ergethidae was based, is not a chordeumid, but a polydesmid.

However, in the following sections, I propose several changes at the family level and numerous generic synonymies, based on studies of specimens of nearly all genera in all known North American chordeumid families, except for the families Caseyidae and Striariidae, currently being revised by other taxonomists. I have also grouped the North American families into superfamilies, and provided names for these taxa. New names were needed because none of these categories are coextensive with previously proposed ones, and do not include any families found outside North America, except in one case. The striking gap between the North American fauna and the very rich European one may be considerably reduced when some of the confusion in names of European chordeumids is cleared up, and it may be possible then to include a few European families in the superfamilies named here, or to use older European names for the superfamilies.

CHARACTERS USEFUL FOR DELIMITING TAXA BELONGING TO HIGHER CATEGORIES IN THE ORDER CHORDEUMIDA

This subject has previously been discussed by Brölemann (1918, 1935), Verhoeff (1906, 1909, 1935), Attems (1959) and Cook and Collins (1895). Only Cook and Collins treated the North American forms in a meaningful way (with specimens on hand), and of the European authors, Brölemann's ideas have best stood the test of time. It is not my purpose here to point out all of the differences and similarities in the various systems, but to evaluate, with respect to the neglected North American fauna, the characters that American taxonomists have used in the past. I want to evaluate these characters according to two main criteria: their possible phylogenetic significance and their applicability in practical taxonomy. For my views on the formation of taxa of higher categories, see the summary below.

NONSEXUAL CHARACTERS

Segment Number

The term segment must be defined for use in the following discussion. In the Diplopoda in general, most trunk segments consist of fused pairs of metameres. According to Manton (1953), this gives maximum body flexibility, pushing power, and tergal area for muscle insertion. However, the first three segments of chilognath millipeds are single metameres. Thus the term segment, as used below and in the taxonomic literature in general, refers to the obvious gross divisions of the trunk and not to the actual derivatives of one metamere. It has been suggested that the term "ring" be applied (Kaestner, 1968), but I think this gives the mistaken impression that all diplosegmental sclerites are fused to form complete body rings, whereas this is really the case only in the Polydesmida. Thus I will continue to use the term segment in this way, with the understanding that it refers to the obvious, usually uniform, divisions of the trunk whether they are actually derived from single metameres or two metameres (diplosegments).

The number of trunk segments is fixed within adults of species in the Order Chordeumida as here considered, as opposed to a variable number within species in the related Order Callipodida. Fixity of adult segment number is probably an advanced character, though Manton (1953) presents some arguments to the contrary for the chordeumids and polydesmids. But fixity of segment number within species is found in all of the more specialized milliped groups, and clearly indicates greater degree of genetic control of development. The actual number of segments present is variable from species to species, and is most likely a function of size, the lesser numbers being an adaptation to small size.

Members of the genus *Branneria* have the fewest segments of any chordeumids (26, a number shared with the European *Chaemosoma*). They are also only 3–4 mm long, the smallest North American chilognaths. Some species of the Trichopetalidae and Tingupidae have only 28 segments, and in the case of some species of *Tingupa*, the males have 28 and the females 30 segments. In all cases of reduction from the basic segment number (30, though some primitive heterochordeumatoids have 32) the animals are small, usually less than 10 mm long, frequently troglobitic, and often have from two to four legless segments at the posterior end of the body, which probably indicates that further reduction is in progress.

Segment number alone as a generic criterion must be used with caution. Brölemann (1918) called the tendency towards a reduced number of segments tachygenesis, and pointed out that Verhoeff's (1913) group Trachyzona, based on genera with reduced segment numbers, was a hodge-podge of unrelated phylogenetic lines that had adapted to small size. *Trichopetalum* (Trichopetalidae) has long been separated from other genera of its family primarily because of a reduced number of segments (28) rather than on characters less subject to adaptive differences, although other genera whose species clearly belong to it have been kept apart from *Trichopetalum*. The presence in some species of *Tingupa* (Tingupidae) of 28-segmented males and 30-segmented females argues strongly against the use of segment number alone as a generic character. *Branneria carinata* (Branneriidae) can be clearly distinguished by gonopod anatomy and secondary sexual modifications as well as its unique segment number; other members of the genus may be found with more, or fewer segments.

I have used segment number as an additional character to group species that are otherwise similar, but have not used it alone.

Troglobitic Adaptations

Adaptations for cave life include loss of pigment, reduction or loss of ocelli, hypertrophy of tactile and chemical sense organs (primarily the antennae), reduction of cuticle sclerotization, hypertrophy (or reduction, in *Pseudotremia*) of segmental setae, and increased length of leg segments. Numerous behavioral and physiological adaptations are also implied. Most taxonomists who work in groups that have troglobitic members agree that these adaptations are not in themselves sufficient to justify lumping troglobites into taxa of higher categories. But in some cases (as in the beetle *Glacicavicola;* see Westcott, 1968) the adaptations are so unique that doubt exists as to which family or genus the animal belongs to, and new families or genera are sometimes described. I know of no such cases in chordeumid millipeds, except possibly the conotylid *Idagona westcotti* Buckett and Gardner, but it is not highly adapted to cave life, and the unusual features are to be found only in the male gonopods. In *Pseudotremia* (Cleidogonidae) there is a series of species, from some having adaptations for leaf-litter surface life to others that are highly adapted troglobites. Without the strong similarities in more stable characters, such as gonopods, the extreme adaptations of the troglobitic species might well lead taxonomists into describing them as belonging to new genera and families.

Troglobitic adaptations are thus not very useful in delimiting families and genera. Perhaps the same might be said of any modification of sense organs (ocelli number, antennal length, etc.), no matter how extreme.

Subdivision of the Mentum

In the past division of the mentum of the gnathochilarium into promentum and mentum in some Chordeumida was considered an important phylogenetic character. Brölemann (1935) used this as one character to distinguish suborders within the order Chordeumida (he considered Callipodida a suborder of Chordeumida, and divided the present Chordeumida into two more suborders on the form of the mentum and characters of the gonopods). The adaptive significance of having the mentum divided or not is obscure. A divided mentum is presumably more flexible. The division is usually on the level of the bases of the lingual laminae. In small forms this division is not at all easy to see, and if the undivided mentum is truncate, the membranous space anterior to it is often mistaken for a promentum.

The absence or presence of this division has been used carelessly. In all keys and other references since 1920 (see especially Chamberlin and Hoffman, 1958), members of the family Trichopetalidae have been characterized as having an undivided mentum, and on this basis have been placed near, or as a subfamily of, the Conotylidae. Cook and Collins (1895) described the promentum in each trichopetalid species they discussed, and all the species examined by me in this study had a divided mentum. I have used this as additional evidence in placing the Trichopetalidae in the Superfamily Cleidogonoidea. Chamberlin and Hoffman (1950) raised the genus *Bactropus* to family status because Cook and Collins described the promentum as "not distinct." The type specimen of *Bactropus conifer* was not examined by Chamberlin and Hoffman, and is apparently lost or destroyed. Likewise, the type specimen of *Conotyla leibergi* probably has the mentum undivided; Cook and Collins (1895) stated that it was divided, and on this alone, Chamberlin (1941b) erected the genus *Cookella.*

This character is clearly not of great adaptive significance. Even if the placements discussed immediately above were based on correct observations, genera and families should not be established on a single character. However, the undivided mentum can be used as a key character to separate species of the Superfamily Heterochordeumatoidea from any other North American chordeumids. Thus the divided mentum is useful at a superfamily level.

Pectinate Lamellae of the Mandible

This character has not been adequately studied. Dissection of the mandibles requires virtual destruction of the head capsule, and so is not advisable on unique specimens. The rows of spines making up the lamellae are difficult to see, even in preparations mounted on microscope slides and examined with phase contrast. I have found the number of lamellae constant within species in those species examined. Smaller species have fewer lamellae. The adaptive significance of the number of lamellae is obscure, and as they are difficult to see and count, I think they are not of much taxonomic utility.

GENITALIA AND SECONDARY SEXUAL MODIFICATIONS

Eversible Coxal Glands

Members of the Order Callipodida and all Colobognatha have eversible coxal sacs on all or most of the legs, for imbibing water from the substrate. In the Chordeumida, these sacs are greatly reduced in number and are found on one or two pairs of legs immediately posterior to the gonopods. They are used not for taking up water, but for receiving the seminal fluid from the genital openings on the coxae of the second legs (Schubart, 1934; Verhoeff, 1910). Secretions presumably formed by the sacs aid in the manufacture of spermatophores, and the tips of the functional gonopods are usually near or actually inserted in these glands. Many preserved specimens have the glands extruded, and often capped with spermatophores. In all the North American chordeumids, the sacs occur on either legs 10 alone, or on legs 10 and 11.[1] This arrangement is consistent within families delimited by other characters, and thus I think distribution of coxal sacs is a conservative character in the Chordeumida that can be very useful in showing relationships.

Postgonopodal and Pregonopodal Leg Modifications

In some chordeumids, from one to all of the seven pairs of pregonopodal legs of the males are modified for grasping the female during mating. The modifications are in the form of enlargement of the legs, sometimes the geniculate form of certain leg segments, and sometimes knobs on the legs. In *Urochordeuma porona* the modifications are quite bizarre. Modifications also occur, primarily in the Cleidogonidae and Conotylidae, in postgonopodal legs. The function of these changes might be to support and make rigid the gonopod complex, and they usually involve the basal articles of the legs and their sternites.

For some reason, it has often been assumed that these modifications are of greater significance than those of the anterior gonopods, and they are frequently mentioned in generic diagnoses (Chamberlin, 1941b; Loomis, 1963). In my revision of the large family Conotylidae, within the genus *Conotyla* I found the differences in pregonopodal leg modifications to be of only species significance; apparently they evolved many times. But in *Austrotyla*, these modifications are uniform in all species of a genus; here I considered them supporting evidence for uniting a group of species, but not as a justification for generic splitting. I have since found that there is a good deal of individual variation in some *Conotyla* species in the distribution of knobs on the pregonopodal legs. In the Trichopetalidae there is variation within a genus in such modifications, but the en-

---

[1] I have been unable to verify the observations of Causey (1963a, 1963b) of small coxal glands on the posterior gonopods (ninth legs) of some Trichopetalidae and Caseyidae, though rudimentary, closed glands occur there in some species of *Cleidogona*.

largement of the pregonopodal legs is most marked in larger species that are not troglobitic, so perhaps there are some relationships between this modification and size. The smallest known *Conotyla* species has the pregonopodal legs completely unmodified.

Loomis (1966) described the genus *Costaricia* (Cleidogonidae), whose species differ hardly at all from those of *Cleidogona.* The distinguishing character used was the apically cleft process of the twelfth sternite. This character does not seem to be of great significance; I believe that species should be lumped in genera based on similarities, rather than differences used for splitting, since genera contain related species. The postgonopodal leg modifications are sometimes of use in separating species of *Cleidogona,* sometimes not. They are uniform in all species of *Pseudotremia.*

I do not think the pregonopodal and postgonopodal leg modifications are of particular use in separating families, though they are sometimes useful characters at the level of genus and species.

Posterior Gonopods

In the Chordeumida, the posterior gonopods are the ninth legpair of adult males, usually modified in some way. Verhoeff (1936) and Attems (1959) thought these structures to be of primary importance in establishing higher categories. The number of articles in the posterior gonopods has been used extensively (see especially Hoffman, 1950a) to delimit genera in the Cleidogonidae, and to a lesser extent in the Trichopetalidae (Causey, 1960a). Buckett and Gardner (1967) considered the absence of posterior gonopod telopodite segments justification for erecting the family Idagonidae for *Idagona westcotti.*

An examination of a series of species of *Cleidogona* or of *Pseudotremia* that are otherwise close indicates that this is a specialized character, perhaps degenerative, permitting a hypertrophy of the anterior gonopods and keeping (in this case) the apparently functionless posterior gonopods out of the way during mating. In some European forms, the posterior gonopods are almost absent. On the other hand, the posterior gonopods, or at least their colpocoxites, function in spermatophore transfer in at least some species of the North American family Conotylidae. But the telopodite articles are reflexed dorsad, out of the way of the colpocoxites. As mentioned above, they are entirely lacking in *Idagona,* and there is a possibility that conotylids with more than two telopodite articles on the posterior gonopods exist.

I think the number of articles in the posterior gonopod telopodites is of only limited value in indicating phylogenetic relationships, but it is of considerable significance which gonopod pair, anterior or posterior, function in spermatophore transfer. The presence or absence of a functional colpocoxite is of particular importance. In some families (Caseyidae, Urochordeumidae), processes occur on the posterior gonopod coxae, but it is not known if they are functional in spermatophore transfer. It is likely that colpocoxites have evolved several times, and there is evidence that originally functional colpocoxites may be displaced in their function by the anterior gonopods (Adritylidae, some species of Conotylidae; see discussion of these families below).

Anterior Gonopods

Unlike Verhoeff and Attems, Brölemann (1935) emphasized the overall morphology of the anterior gonopods, and arrived at a much more satisfactory classification of the European chordeumids. Only recently has the value of the anterior gonopods in grouping species and genera been recognized in the United States (Hoffman, 1961). Of great importance is the degree to which the anterior gonopods have departed from their original leglike form through the fusion of articles of the individual legs and through the bilateral fusion of the primitive eighth legpair. Hoffman (1963) studied some species of the family Heterochordeumatidae in detail. The anterior gonopods are extremely leglike, though reduced in size, and the posterior gonopods bear colpocoxites remarkably like those found in the family Conotylidae. The gonopod morphology of species of the Heterochordeumatidae is the most leglike, and thus the most primitive, yet discovered among the Chordeumida.

In most families that occur in Europe, the anterior gonopods are completely fused to each other, and show few traces of segmentation. Median structures of obscure derivation are common. In many species, extreme reduction in the number of articles in the legs immediately anterior and posterior to the gonopods has also taken place. Few North American species are so highly specialized. In species of the Trichopetalidae, the coxae of the anterior gonopods are free from the sternite, and the telopodites, though single-articled, are articulated, not fused, with the coxae. Conotylids belong to the group of families in which the colpocoxites of the posterior gonopods are functional—the anterior gonopods are reduced to single articles but are free from the sternite. In one species (*Achemenides pectinatus*) the anterior gonopod coxae are fused bilaterally.

In species of the Cleidogonidae, the anterior gonopods are much modified, but coxal and telopodite regions can still easily be distinguished, especially if homologies with gonopods of species of the Trichopetalidae are recognized; the posterior gonopods are not functional. In members of the superfamily Brannerioidea, for example *Branneria,* a great amount of fusion has taken place, and there are median structures. Some others in that superfamily, however, have still-discernable coxal and telopodite regions (Tingupidae). In the species of the family Adritylidae, though the basic conotyloid morphology is present, cheirites, formed from the complete fusion of gonopod, sternite, and tracheal apodeme, occur. The posterior gonopod is possibly not functional, and the tenth pair of legs is modified to form a supporting structure.

Gonopod morphology of all the North American families is discussed in more detail in another section. But as can be seen by the preceding discussion, the gonopod anatomy is of great phylogenetic and therefore taxonomic importance. The structure must be studied in detail when new taxa are proposed, since superficial similarities in body form and other characters have led to unnatural placements in the past.

Female Genitalia

The cuticular specializations around the openings of the oviducts have been termed *cyphopods.* Their origin was at first the subject of some debate; without any real evidence, Verhoeff (1909) claimed that these valvelike structures were the reduced posterior leg pair of the third segment. Brölemann and Lichtenstein (1919) demonstrated that they were merely specialized regions of integument developed around the oviduct pores and connected to the coxae of the second pair of legs; they showed that the same is true of the so-called penes found in male millipeds in the same position. The third segment is a single metamere. Wood (1865) used the shape of the cyphopods as a species character in the family Parajulidae, and later Brölemann (1922) studied them in detail and found an abundance of differences between species. Keeton (1960) found them useful in the family Spirobolidae. In the chordeumids, their usefulness varies. Brölemann used them extensively in his treatment of the Order Chordeumida in *Faune de France* (1935), but frequently depended on small details that might prove unreliable when large series of specimens are studied. In the Conotylidae, I found the cyphopods too variable within species to be useful as a species character (Shear, 1971a), but in *Cleidogona* and *Pseudotremia* (Cleidogonidae) they are extremely useful.

However, the general plan is too similar in all millipeds to be of much utility in separating families and genera.

SUMMARY

From the brief discussion above, and the more detailed descriptive material to be found in the section on superfamilies, the following points are clear.

1. The gross morphology of the gonopods, particularly the degree of segmentation in the anterior gonopods, and the functional distinction between anterior and posterior gonopods, are of paramount importance in placing species in the proper genera and families, and in relating families to each other.

2. Other characters should be used in connection with the gonopod morphology, but with caution, and with the understanding that many of them are subject to convergent evolution because of their obvious adaptiveness.

3. *Genera and families are composed of similar species grouped together to emphasize that similarity.* Monotypic higher taxa are logically justifiable, however, if it can be shown that the included species would make other genera and families in which they might be placed obviously polyphyletic, or if the included species can be demonstrated to be the end of a separate phyletic line. Both of the above criteria rely primarily on inference from taxonomic information.

It is not inconsistent to have within the same major group very large, presumably recent, actively speciating taxa (*e. g.*, *Cleidogona*) and probably very old, nearly extinct, monotypic ones (*e. g.*, Adritylidae). The genus is not an objective category, but neither should it be arbitrary, in composition or size.

Keys to Superfamilies and Families of North American Chordeumida

Key to Superfamilies

1a. Mentum not divided .... HETEROCHORDEUMATOIDEA
1b. Mentum divided (Fig. 181) 2
2a. Both coxae 10 and 11 of males with gland openings .... CLEIDOGONOIDEA
2b. Coxa 10 only with gland opening 3
3a. Coxae of male anterior gonopods with articulated flagelliform branch (Fig. 429); posterior gonopods 2-segmented, apical segment flattened (Fig. 430) .... STRIARIOIDEA
3b. Coxae of male anterior gonopods without such a branch, telopodites (Fig. 465) flagelliform; posterior gonopod 3–4-segmented, apical segment not flattened (Fig. 472) .... BRANNERIOIDEA

Key to Families of Heterochordeumatoidea

1a. Leg 10 of males of normal size .... CONOTYLIDAE
1b. Leg 10 of males reduced (Fig. 496) .... ADRITYLIDAE

Key to Families of Cleidogonoidea

1a. Posterior gonopods of males clavate distally (Fig. 507) .... TRICHOPETALIDAE
1b. Posterior gonopods of males attenuate distally (Figs. 387, 413) .... CLEIDOGONIDAE

Key to Families of Striarioidea

1a. Collum partially covering head 2
1b. Collum not covering head 3
2a. Body segments with prominent paranota (Fig. 452) .... RHISCOSOMIDIDAE
2b. Body segments without paranota; 10–12 longitudinal ridges on each segment (Fig. 425) .... STRIARIIDAE
3a. Body segments with prominent paranota (Fig. 446) .... UROCHORDEUMIDAE
3b. Body segments cylindrical .... CASEYIDAE

Key to Families of Brannerioidea

1a. Adults with 26 segments BRANNERIIDAE
1b. Adults with 28 or 30 segments .... TINGUPIDAE

Artificial key to families of the Order Chordeumida in North America

I have attempted to base the following key on nonsexual characters, but in some cases, this was not possible. In such instances, gonopod characters that can easily be observed under low magnification have been used.

1a. 26 postcephalic segments BRANNERIIDAE
1b. 28–30 postcephalic segments 2

2a. Body segments with series of heavy, longitudinal, linear carina (Fig. 425), but otherwise circular in cross section; males with prominent spines on the labral angles ..... STRIARIIDAE

2b. Body without such carina, or not circular in cross section, with enlarged lateral tubercles (Fig. 6) or polydesmidlike paranota (Fig. 446); males without labral spines 3

3a. Mentum divided into mentum and promentum (Fig. 181) 4

3b. Mentum not divided 9

4a. Body segments with rather broad, flat polydesmidlike paranota; dorsal surface with various kinds of sculpturing, but never smooth 5

4b. Body segments cylindrical, *or* with more or less prominent enlarged lateral tubercles, but not polydesmidlike paranota; dorsal surface usually smooth, but sometimes (*Pseudotremia*) with coarse knobs (Fig. 6) between the lateral tubercles 7

5a. Collum broader than the head; dorsal body surface with closely set, sharp-pointed tubercles (Fig. 452) RHISCOSOMIDIDAE

5b. Collum narrower than head; dorsal surface otherwise 6

6a. Anal segment trilobed; paranota (Fig. 446) broad, thin, not curved ventrally, lateralmost seta in a midmarginal notch on paranota; adults *ca.* 16–20 mm long ..... UROCHORDEUMIDAE

6b. Anal segment not trilobed; paranota (Fig. 460) narrowed distally, thick, curved ventrally, lateralmost seta on posterior side of paranota; adults less than 10 mm long ..... TINGUPIDAE

7a. Posterior gonopods of males (Fig. 444) 2-segmented, basal segment (coxa) with a strong mesal process (coxite) CASEYIDAE

7b. Posterior gonopods of males 2–6-segmented (Figs. 387, 413, 504), but 2-segmented gonopods lacking a coxite 8

8a. Posterior gonopods 2-segmented (Fig. 504), distal (telopodite) segment enlarged; small animals (less than 10 mm long); antennae usually clavate ..... TRICHOPETALIDAE

8b. Posterior gonopods (Figs. 387, 413) more than 2-segmented, distal segments smaller than basal; larger animals (usually more than 10 mm long); antennae long, not clavate ..... CLEIDOGONIDAE

9a. Tenth legs of males (Fig. 496) with coxae enlarged, telopodite greatly reduced ..... ADRITYLIDAE

9b. Tenth leg telopodites normal, coxae sometimes slightly enlarged ..... CONOTYLIDAE

Superfamily STRIARIOIDEA Cook, NEW STATUS

Striarioidea Cook, 1889, Proc. U. S. Natl. Mus., 21: 670.

Chordeumid millipeds with 30 segments; mentum divided. Anterior gonopods complex, with two or more distinct coxal branches, at least one of which is flagelliform and may be movable. Telopodites lobelike, usually not fused to coxae. Posterior gonopods with sternum broad, coxae with or without processes, two or three telopodite segments, expanded and flattened. Coxae of legs 10 with glands. North America.

Included families. Striariidae Bollman, 1888; Caseyidae Verhoeff, 1909; Rhiscosomididae Silvestri, 1909; Urochordeumidae Silvestri, 1909.

Discussion. The name Striarioidea was used by Cook (1899) as a subordinal name under his Order Coelochaeta, though the spelling now conforms to superfamily names, which covered our present orders Chordeumida and Callipodida. It originally contained only the family Striariidae, and this arrangement was long accepted by milliped taxonomists, on the basis of the peculiar body form (the collum is hoodlike, the anal segment trilobed, the metazonites, with prominent ridges, and apparently lacking the usual segmental setae; sexual dimorphism is pronounced), but Causey (1963a) examined the gonopods and found the subordinal designation unwarranted. I agree, if the category Striarioidea, at whatever level, includes only the family Striariidae. However, Causey's statement was based on an erroneous interpretation of the anterior gonopods, discussed under the Family Caseyidae below. The Caseyidae and Striariidae are related, but not for the reasons Causey (1963a) puts forth. A detailed examination of material of two other poorly known families, Rhiscosomididae and Urochordeumidae, makes it possible to include them in this assemblage. The main points of similarity are covered in the characterization above, but to reinforce this new status of the name Striarioidea, some further discussion of the similarities of the striariids to the other families is needed.

The members of the family Rhiscosomididae are heavily sclerotized, and have the collum wider than, and partly concealing, the head—in these characters they resemble the species of *Striaria.* In *Urochordeuma* (Urochordeumidae) the anal segment is trilobed as it is in the striariids, and the body is moderately heavily sclerotized. Urochordeumids resemble rhiscosomidids in the broad, thin paranota; but like the species of the family Caseyidae, the head is free from the collum and there are lateral striations. Thus a number of the characters previously thought of as unique to the Striariidae have their analogues in other related families. The ridges of the dorsum and the labral spines and modified mandibles of male striariids remain as unique characters of that family. Though none of the specimens of *Striaria* I have examined have detectable segmental setae, *Speostriaria shastae* has them long and prominent.

The distribution of the superfamily as it is now known is primarily western. The several genera of Caseyidae are found on the Pacific coast, with a single genus (*Underwoodia*) in New England and Newfoundland. *Urochordeuma* has two possible species in the region of Mt. Tacoma, Washington. The three known species of *Rhiscosomides* are found in southern Oregon and the San Francisco Bay area of California. Species of the Striariidae are known from both the Pacific coast and the Appalachian Mountains, from northern Virginia and southern Indiana to Georgia. It must be emphasized that this section of the Order Chordeumida is in the greatest need of critical study, but the scarcity of specimens will postpone such work for some years.

The relationships of the superfamily Striarioidea are very obscure. The caseyids are similar to the cleidogonids in general body form. However, the development of coxal processes on the posterior gonopods of some species may indicate a relationship with the Heterochordeumatoidea. The complexity and anatomy of the anterior gonopods suggest a relationship with the Brannerioidea. Whichever of the other three North American superfamilies the group is related to, it is clear they have had a long separate history.

Family STRIARIIDAE Bollman

Striariidae Bollman, 1893, Bull. U. S. Nat. Mus., 46: 158; Cook, 1899, Proc. U. S. Nat. Mus., 21: 668; Causey, 1958, Proc. Biol. Soc. Washington, 71: 179 (key to genera).

Type genus. Striaria Bollman, 1888.

Included genera. Striaria, Amplaria, Vaferia, Speostriaria.

Range. California, Oregon, Indiana, Appalachian Mts. from Virginia to Georgia.

Diagnosis. This family is set apart from all other North American chordeumids by the hoodlike collum and peculiar sculpture of the tergites (Fig. 425).

Description. Antennae of moderate length (Fig. 425), not clavate. Ocelli present, usually less than 12, irregularly arranged. Mentum divided. Segments 30, metazonites with 10–12 sharply elevated longitudinal ridges, the lateralmost pair at ventral segment margin, areas between ridges with small tubercles. Collum broad, expanded, wider than head, hoodlike, partly covering head (Fig. 425). Anal segment trilobed. Segmental setae present or absent. Males usually with long, immovable spines at labral margins. Anterior gonopods: sternum broad, well sclerotized, expanded and flaring laterally (Figs. 426, 427). Coxae divided into two or three branches, anteriormost rodlike (Fig. 428), posteriormost forming sheath for flagelliform branch (Fig. 429); telopodites irregular, globular, distally with minute scales. Posterior gonopods: 2-articled, distal article expanded and flattened (Fig. 430), sternum broad, with platelike posterior process. Pregonopodal legs thickened, crassate, curiously flattened. Third coxae with large, flasklike anterior projections. Coxae 10 with glands, but not much enlarged.

Discussion. This family may be quite large in number of species (R. L. Hoffman, personal communication), but because of the humus-dwelling habits and a definite tendency to occur in drier habitats where millipeds are not usually searched for, species of the family Striariidae are rare in collections. The family Striariidae is currently being revised by Dr. J. P. Mauries. The criteria by which genera have been separated are, as a rule, unreliable. Causey (1958) pointed out that the presence of 12 crests on the collum is not diagnostic of *Amplaria,* as Chamberlin (1941b) stated in describing that genus. Causey continues to recognize *Amplaria,* however, on the basis of its fewer ocelli and a deep transverse furrow on the collum. I have not seen specimens of this genus. *Vaferia* (Causey, 1958) is separated on the basis of the anterior flattening of the body, and the lack of labral spines on the males. Causey also described *Speostriaria* (Causey, 1960) for the very large, troglobitic species *Speostriaria shastae.* Except for the matter of greater sexual dimorphism, all the characters mentioned as diagnostic of *Speostriaria* are due to troglobitic adaptations. The small gonopod differences do not seem to justify generic distinction.

I examined the gonopods of three Appalachian species in detail. It appears to be impossible at this time to assign names to these forms, but I have illustrated a male from Shenandoah National Park that is probably referable to *Striaria columbiana* Cook.

In lateral view (Fig. 427), the heavily sclerotized sternum (*S*) bears a lateral projection that is set off by a suture and conceals the tracheal spiracle. The anterior coxite (Fig. 428) is complexly branched; the details of this branching appear to be of value in distinguishing species. The transverse ridges seen on this branch in anterior view (Fig. 426) are characteristic of the species of *Striaria* I examined. The posterior branch, seen in Figure 429 in mesal view, is articulated basally with a movable flagelliform branch (*F*). The number of flagella appears to be variable. Distally, this posterior coxite forms a curved sheath. The telopodites (*T*, Figs. 426, 427) are lobelike and curve posteriad and dorsad, where they are closely set with minute scales. The anterior portion of the telopodite (*T*, Fig. 426) may actually be the body of the coxa. It is muscularized directly from the tracheal apodemes.

Family CASEYIDAE Verhoeff

Caseyidae Verhoeff, 1909, Zool. Anz., 34: 567; Causey, 1963, Wasmann J. Biol., 21: 193.
Underwoodiidae Verhoeff, 1909, Zool. Anz., 34: 568.

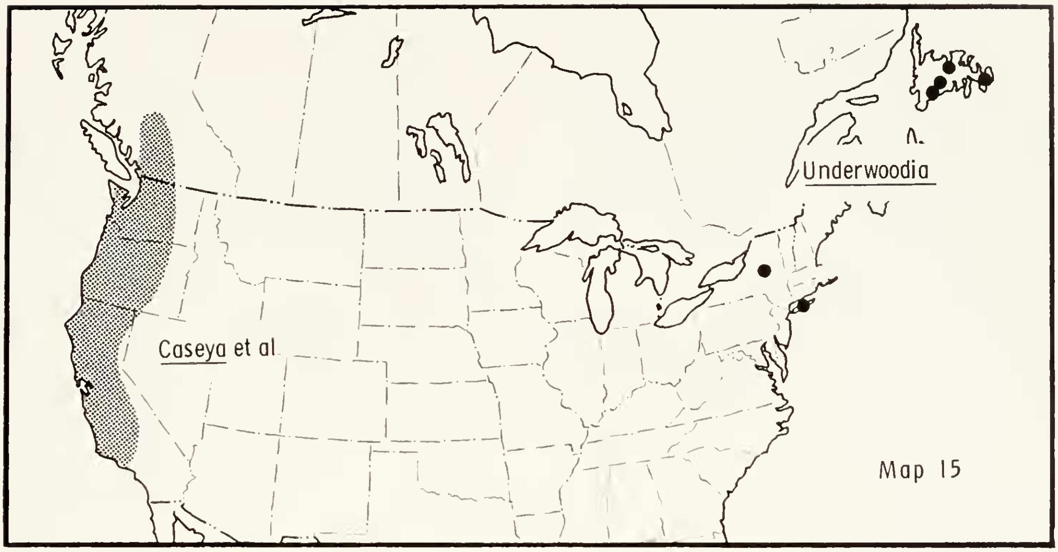
Type genus. Caseya Cook and Collins 1895.

Included genera. Caseya, Opiona, Placerna, Speoseya, Vasingtona, Zantona, Underwoodia.

Range (Map 15). Newfoundland, Long Island, northern New York State, (*Underwoodia*); northern California, Oregon, Washington, British Columbia. Two species of *Underwoodia* were described by Chamberlin from Utah (*U. hespera* and *U. tida*). The female holotype of *hespera* was recently found in the collection of the MCZ; it is an immature female and is probably not an *Underwoodia.* The type of *U. tida* is also a female.

Diagnosis. The body segments are cylindrical and have lateral striations, but are dorsally smooth. The collum does not cover the head.

Description. Antennae of moderate length, not clavate. Ocelli present or absent. Mentum divided. Segments 30, prominent carinae or tubercles lacking, body cylindrical, segments with prominent lateral striations. Anterior gonopods (Figs. 431–433): sternum distinct, well sclerotized. Coxae separate, subglobular; coxites extremely complex, usually with 2–4 dis-



Map 15. Central North America, showing distribution of western genera of Caseyidae (*Caseya* et al., hatched area) and the genus *Underwoodia* (dots).

tinct divisions. Flagella usually present; telopodite simple or with a rudimentary suture. Posterior gonopods (Fig. 434) 2-articled; telopodite article enlarged, coxa with prominent coxite and sometimes a small gland. Modifications of pregonopodal legs various, but usually with coxal projections on legs 2 and 3, coxae of legs 7 enlarged, lobed, posteriorly excavate. Coxae of legs 10 enlarged, lobed, with large gland.

Discussion. This family, very probably a large one in number of species, is the most poorly known of abundant North American milliped families. It is currently the subject of a revision being carried out by Mr. Michael Gardner, Davis, California, and for that reason, I am limiting the present discussion to the gonopod structure of *Caseya heteropus* Cook and Collins, and some past misconceptions regarding the Caseyidae.

Verhoeff (1909) probably did not have specimens when he set up separate families for Cook and Collins' (1895) genera *Underwoodia* and *Caseya*. Causey (1963a) suggested that there was no reason for keeping the two families separate, an opinion with which I concur, despite the fact that the extreme rarity of *Underwoodia* males has not allowed me to examine their gonopod anatomy; the sex ratio in *U. polygama* (= *U. iuloides*?) is about 40:1 in favor of females (Cook and Collins, 1895; Palmén, 1952), and the animals themselves are uncommon, and boreal and hygrophilous in habit. The holotypes of both *U. polygama* Cook and Collins and *U. iuloides* (Harger) have been lost.

However, I cannot find any evidence in *Caseya heteropus* to support Causey's (1963a) interpretation of the gonopods of *Opiona* and *Speoseya*, which she extends to the whole Family Caseyidae, and by implication to the family Striariidae. Briefly, she asserts that what are here referred to as the anterior gonopods actually represent both anterior and posterior gonopods, closely appressed, and that what are here called posterior gonopods are actually the tenth legs. Causey presents no sound evidence for this view, but I suspect that the tiny coxal gland on the posterior gonopods of *Speoseya grahami* and *Opiona siliquae* strongly influenced Causey's interpretation. But an examination of Palmén's (1952) excellent figures of *Underwoodia polygama* rules out such an interpretation of the gonopods of that species; thus to propose for caseyids such an unusual gonopod structure, in fact a unique one, and at the same time combine the family with *Underwoodia* is inconsistent.

I examined the gonopods of *Caseya heteropus* in detail, and found no evidence that two pairs of legs are involved in the anterior gonopods. In fact, the musculature and structure of the sternites militates against such a view. If indeed the "posterior gonopods (of Causey)" are closely appressed and fused with the "anterior gonopods," they have lost all independent muscularization as well as their sternite and tracheal apodemes. I have not known such a development to have occurred anywhere in the Diplopoda. I must then assume that Causey considered the telopodites of the anterior gonopods (Fig. 431, *T*) to be "posterior gonopods"; this is an understandable error in view of the complexity of the anterior gonopod coxites (Fig. 432, *C*).

The complex pre- and postgonopodal leg modifications have been described in detail for this species by Cook and Collins (1895) and need no further attention. They have been the basis for division of the family into genera, which may have to be re-aligned after detailed study of the various species involved. The affinities of this family are very obscure, but relationship with the Striariidae is clear. There may be a distant kinship to the trichopetalid-cleidogonid complex, but much more must be learned about the gonopods and their function before this can be settled with any certainty.

Family UROCHORDEUMIDAE Silvestri

Urochordeumidae Silvestri, 1909, Rend. R. Accad. Lincei, 5: 229; 1913, Boll. Lab. Zool. Gen. Agr. Portici, 7: 303; Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull., 212: 107.

Type genus. Urochordeuma Silvestri, 1909; family monobasic.

Range. Vicinity of Mt. Ranier, Pierce and King counties, Washington.

Diagnosis. The head is wider than the collum, not narrower, as it is in the Rhiscosomididae; the paranota (Fig. 446) separate this family from the Caseyidae.

Description. Antennae long, slightly clavate. Ocelli present, in trapeziform group. Mentum divided. Segments 30, most with prominent, polydesmidlike paranota (Fig. 446) that more than double body width; prominent lateral striations. Anal segment trilobed. Body surface with scattered, prominent tubercles; posterior margins of midbody segments with row of strong rugae. Gonopods: anterior gonopods (Figs. 447, 448) with a separate, well-sclerotized sternum (Silvestri, 1913); gonopods not bilaterally fused but apparently without clear separation of coxa and telopodite. Flagellum present. Posterior gonopods (Fig. 445) 2-articled; telopodite article enlarged, coxa with process. Modifications of pregonopodal legs as described for *Urochordeuma.* Coxae of legs 10 with coxal gland; coxae of legs 11 enlarged, shallowly excavate on anterior surface.

Discussion. This unusual family has been a source of confusion since its description. Most recently, Attems (1959) separated it from all other chordeumid families because Silvestri's (1913) drawings show the vas deferens opening separately anterior to the second coxae. This was a mistaken observation on the part of Silvestri, one which he also repeated in the same paper for *Rhiscosomides mineri.*[1] The body form is very similar to that of *Diplomaragna* (Attems, 1898; Murakami and Paik, 1968), but the gonopods point to a relationship with the Caseyidae.

Only two species are known, *Urochordeuma bumpusi* Silvestri, 1909, and *U.*

---

[1] Actually, since it is not indicated whether the view given by Silvestri is anterior or posterior, it would be impossible to say that the openings were anterior to the coxae.

porona Chamberlin, 1941. Both are from the vicinity of Mt. Ranier, Washington, and are so similar in description that they may very well represent the same species, but I will not combine them without examining specimens of *U. bumpusi;* the types have apparently been lost. The gonopods of *U. porona* could not be studied in detail from the unique holotype. During the original dissection, the basal region of the anterior gonopods was damaged. The left gonopod was missing altogether. The labels on Figures 447 and 448 are thus speculative, based on the obvious similarity to the gonopods of *Caseya.* The coxites (*C,* Figs. 447, 448) are complex and folded to enclose a single flagellum arising from the anterior margin. The telopodite (*T,* Fig. 448) is simple and partly fused along its anterior edge to the coxite. The basal region of the coxa bears a prominent group of setae. The peculiar modifications of the anterior legs have been described by Chamberlin (1941). The second legs have long processes on the third segments (Fig. 449), and the third legs have long knobs arising from the coxae (Fig. 450), similar to the processes found in *Striaria.* The seventh coxae have lobes similar to those found in *Caseya.*

Family RHISCOSOMIDIDAE Silvestri

Rhiscosomididae Silvestri, 1909, Rend. R. Accad. Lincei, 18: 232; 1913, Boll. Lab. Zool. Portici, 7: 307.

Type genus. Rhiscosomides Silvestri, 1909.

Diagnosis. The only chordeumid milliped family in North America other than the Striariidae with the collum wider than the head; the dorsum bears densely scattered sharp-tipped tubercles, rather than the longitudinal ridges of the Striariidae.

Description. Thirty segments. Mentum divided. Head narrower than collum (Fig. 451). Antennae short, clavate. Ocelli present, in an irregular single or double row. Postcollum segments (Fig. 452) with broad, almost polydesmidlike paranota; dorsum with dense scattering of sharp-tipped tubercles. Pregonopodal legs of males enlarged, not otherwise modified. Anterior gonopods (Figs. 453–456): sternum strongly sclerotized, laterally expanded. Coxae with 2 groups of coxal processes, the anteriormost sometimes fused to form a plate, the posteriormost with flagelliform processes and scalelike setae. Telopodites simple, lobelike. Posterior gonopods (Figs. 457, 458): sternum bandlike, strong, laterally rugose. Coxae large, expanded, rugose. Telopodite article lobelike. Coxae of legs 10 with glands. Twelfth sternum and legs normal.

Distribution. Pacific coast of North America (Map 16).

Discussion. Very little is known about this family. Silvestri (1913) described *Rhiscosomides mineri* from Lebanon, Linn County, Oregon. I have seen a female from Santa Cruz County, California, and a collection of immature males from Loon Lake, Douglas County, Oregon. The second species of the family known from males is described here as *R. acovescor,* from Marin County, California. The collecting labels on all specimens I have seen indicate that the animals live in conifer duff. The Rhiscosomididae and Striariidae seem more closely related to each other than to the Caseyidae; but I hesitate to combine them, with so little known about the eventual extent of the families.

Each described species is discussed in more detail below.

Genus *Rhiscosomides* Silvestri

Rhiscosomides Silvestri, 1909, Rend. R. Accad. Lincei, 18: 232.

Type species. Rhiscosomides mineri, by monotypy. The gender of the generic name is neuter.

Rhiscosomides mineri Silvestri

Rhiscosomides mineri Silvestri, 1913, Boll. Lab. Zool. Portici, 7: 308, figs. 4–7, ♂.

Types. Male holotype from a rotting tree, Lebanon, about 30 mi. south-southwest of Salem, Linn Co., Oregon; whereabouts of types unknown.

Discussion. Loomis (1966) reported that Silvestri had sent him a syntype, but it could not be located. Silvestri's 1913 figures of *Urochordeuma bumpusi,* described in the same paper, are reasonably accurate, but *R. mineri* is a much smaller form, and the figures of the gonopods do not much resemble those of *R. acovescor* presented here. The immature males mentioned above from nearby Loon Lake, Douglas County, Oregon, are probably *R. mineri,* since they all have five ocelli. A redescription of this species from males is badly needed.

Rhiscosomides josephi Chamberlin

Rhiscosomides josephi Chamberlin, 1941, Bull. Univ. Utah Biol. Ser., 6: 16–17.

Types. Female holotype from John Day Creek, Douglas Co., Oregon, collected 18 November 1941 by J. C. Chamberlin, deposited in University of Utah collection, examined.

Discussion. The "differences" between this species and *R. mineri* given by Chamberlin in his extremely brief description are quite useless — for example, the coloration is described as "brown rather than chestnut." However, the type has seven ocelli as opposed to five in *R. mineri,* and ocelli number may be a good species character in *Rhiscosomides;* a large collection of immature males I have assigned to *R. mineri* all have five ocelli on both sides of the head.

Rhiscosomides monterea (Chamberlin) NEW COMBINATION

Tingupa monterea Chamberlin, 1910, Ann. Ent. Soc. Amer., 3: 240–241, figs. 3–5, probably ♀.

Type. Holotype of unspecified sex from Pacific Grove, California, coll. June, 1902, lost, presumed destroyed.

Discussion. It is clear from several points in the discussion of nonsexual characters of this species given by Chamberlin (1910) that it belongs in *Rhiscosomides* and not *Tingupa.* In particular, the sharp-tipped dorsal tubercles, denticulate paranota, and light spots around the bases of the segmental setae place it here; the type was also reported as having eight ocelli. A female *Tingupa* from Marin County, California, has 13 ocelli, but female *Rhiscosomides* from San Mateo County have only eight, and I have assigned these latter specimens to *R. monterea.*

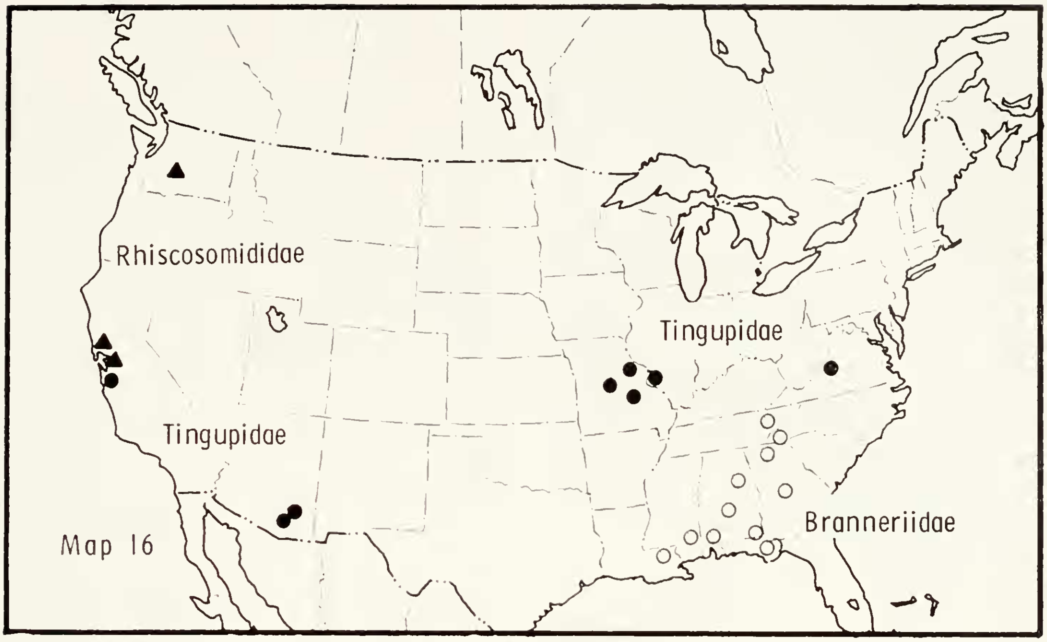
Rhiscosomides acovescor n. sp.

Figures 451–458

Types. Male holotype, a second male, and females and immature specimens from *Sequoia* duff, S. P. Taylor State Park, Marin Co., California, collected 7 January 1962 by C. W. O'Brien. The specific epithet is a Latin noun in apposition and means "needle-eater," in reference to the species' habitat.

Diagnosis. Distinct from *R. josephi* and *R. monterea* in ocelli number; and from *R. mineri* in details of the gonopods.

Description of male holotype. Length, 5.8 mm, width 1.3 mm. Five ocelli in 2 rows of 3 and 2. Head (Fig. 451) broadly rounded, depressed in anterior midline and with two supra-antennal swellings. Antennae strongly clavate, antennal segment 5 longest and thickest. Midbody segments (Fig. 452) typical for genus. Coxae of leg 7 enlarged, pregonopodal legs slightly more crassate than other legs. Anterior gonopods: sternum (*S,* Fig. 453) bandlike, laterally expanded, tracheal spiracles mesal, below corresponding prongs on gonopod coxite. Coxae with two groups of coxites; the anteriormost (*C,* Fig. 453) fused along midline to form thin anterior plate, with strongly projecting anterior hooks that fit into sockets at tracheal spiracles. Posterior side of plate gives rise to paired, flattened flagellae formed from fusion of numerous sclerotized fibers. Posterior coxite (*C,* Fig. 456) basally lobe-



Map 16. United States, showing distribution of the families Tingupidae (dots), Rhiscosomididae (triangles), and Branneriidae (circles).

like, with scalelike setae and a posterior flagelliform branch. Telopodites (*T*, Fig. 454) simple, lobelike, well muscularized from tracheal apodeme and coxae. Coxae of legs 10 enlarged, with glands. Posterior gonopods: as described for genus (Figs. 457, 458).

Notes. The gonopods of *R. acovescor* do not agree well with Silvestri's figures of *R. mineri*, but these figures are difficult to interpret. It is possible that more than one genus is involved in *Rhiscosomides*.

Superfamily BRANNERIOIDEA Cook, NEW STATUS

Chordeumid millipeds with 26–30 segments; mentum divided. Anterior gonopods complex, of various forms, but always with one or more prominent colpocoxites and a distinct, posterior telopodite region. Posterior gonopods with reduced number of segments, but without colpocoxites. Coxae of legs 10 and 11 with glands, or with the front faces excavate (*Branneria*). North America.

Included families. Branneriidae Cook, 1896; Tingupidae Loomis, 1966.

Discussion. It is questionable whether this superfamily really represents a monophyletic line, despite the similar gonopod plans. The similarities of the included families may be the result of convergent evolution from several lines and due to adaptation to small size. But they are incompletely known, both with regard to the numbers of genera and species involved and their respective distributions. *Branneria* (Branneriidae), for example, has only been reported in the literature once since its description, but actually it is widespread in the southeastern United States (Map 16), and extremely common at certain localities. Most species of *Tingupa* (Tingupidae) are known only from the type locality, though *T. pallida* is known from several localities in Missouri and Illinois (Map 16).

The fact that the two included families both lack posterior gonopod colpocoxites, have glands on coxae 10 and 11, and have the mentum divided, may eventually relate them to the Cleidogonoidea, but it is obvious that these families have had a long separate history.

There are a few European genera that superficially resemble the North American families grouped here, especially in the complexity of their gonopods and their small size. I have been able to study specimens of some of these genera, through exchange collections placed in the MCZ by Verhoeff and Attems. *Chaemosoma* (specimen examined) and *Acrochordum* (Strasser, 1942; Attems, 1898) have anterior gonopods superficially like those of *Rhiscosomides* and *Tingupa*, respectively, but also have more or less complex colpocoxites on the posterior gonopods. The gonopod construction of *Halleinosoma* (Schubart, 1934) is quite close to that of *Branneria*. But *Branneria* has 26 segments, as opposed to *Halleinosoma's* 30, and the tenth and eleventh legs of *Branneria* are much more reduced than those of *Halleinosoma*. These differences may be only of generic importance, and if this is so, *Halleinosoma* should be transferred to the family Branneriidae.

The literature on the European fauna is in too great a state of confusion, owing mostly to complete disregard on the part of the prolific K. W. Verhoeff for the rules of priority in nomenclature, for any statement to be made about their position in the system proposed here until a new, complete and detailed study of specimens is carried out.

Family TINGUPIDAE Loomis

Tingupidae Loomis, 1966, Proc. Biol. Soc. Washington, 79: 227.

Type genus. Tingupa Chamberlin, 1910. The family is monobasic.

Diagnosis. Distinct from the Branneriidae in having 28 or 30 segments as opposed to 26, and from the Rhiscosomididae in having the collum much narrower than the head.

Description. Twenty-eight or 30 segments. Mentum divided. Head wider than collum. Antennae short, markedly clavate (Fig. 459). Ocelli present, but reduced in some species. Postcollum segments with thick paranota (Fig. 460); dorsum with heavy sculpturing of short, sharp-edged ridges. Pregonopodal legs of male not modified, sometimes slightly more crassate than other legs. Anterior gonopods (Figs. 461, 465): sternum small, bandlike; coxae with mesal and lateral coxites touching to form an anterior plate; coxites with spinose processes distally; telopodites with 2 flagelliform branches. Posterior gonopods (Figs. 464, 472): usually 4-segmented, fourth segment minute. Coxae of tenth and eleventh legs with coxal glands. Twelfth legs and sternum not modified.

Distribution (Map 16). North America, primarily southern half of United States — California, Utah, Arizona, Missouri, Illinois; Virginia? Florida?

Discussion. The family contains the single genus, *Tingupa*. There may be other genera, however; immature 28-segmented females that greatly resemble *Tingupa* in general appearance have been collected in Montgomery County, Virginia. They are minute (3 mm long), totally without pigment and blind. Loomis (personal communication) has collected immature and female tingupids in Florida,[1] and I have seen immature *Tingupa* from Marin County, California. The distribution of the family (Map 16) is incompletely known. None of the species have ever had their gonopods adequately illustrated, thus each of the three described species is discussed in more detail below. *Tingupa monterea* Chamberlin (1910) is, judging by the description, obviously not a *Tingupa* but a *Rhiscosomides;* the type has been lost.

---

[1] New evidence indicates these specimens probably belong to *Branneria*.

Genus *Tingupa* Chamberlin

Tingupa Chamberlin, 1910, Ann. Entomol. Soc. Amer., 3: 238.

Type species. T. utahensis, by original designation. The gender is believed to be feminine.

Key to Species of *Tingupa*

1a. Males with 30 segments; caves in Missouri and Illinois .... *pallida*
1b. Males with 28 segments; (females with 30) 2
2a. Gonopods as in Figs. 465–467; ocelli 10–17; Arizona .... *arizonica*
2b. Gonopods as in Figs. 459–464; ocelli about 20; Utah .... *utahensis*

Tingupa utahensis Chamberlin
Figures 459–464

Tingupa utahensis Chamberlin, 1910, Ann. Entomol. Soc. Amer., 3: 238, pl. 33, figs. 3–8 (sex not indicated).

Types. Sex of holotype and paratypes not specified, from Mill Creek Canyon, Salt Lake Co., Utah; presumed lost. I studied a series of specimens collected at the type locality 25 May 1924 by R. V. Chamberlin, and identified by him as *T. utahensis*. Specimens deposited in MCZ.

Discussion. Chamberlin (1910) accurately and in great detail described the anatomy of *T. utahensis,* probably from a female. The nonsexual characters of the males are nearly identical to those of the female, but males are somewhat smaller (6–7 mm long, 0.9 mm wide) and have only 28 segments. Both sexes are uniform dark brown after long preservation, and are heavily sclerotized. Loomis (1966) assumed that *T. utahensis* males were 30-segmented, reasoning from *T. pallida. Tingupa utahensis* is very close to *T. arizonica,* there being only minor differences in the gonopods. Chamberlin (1925) gave the name *T. utahensis australis* to a female specimen from "the canyon," Cedar City, Iron County, Utah (holotype in MCZ, examined). The status of this form is not clear in the absence of males. I think it is likely that *T. utahensis* and *T. arizonica* are parts of a widely distributed polytypic species. *Austrotyla coloradensis* (Conotylidae) has a distribution nearly as wide.

Tingupa arizonica Loomis
Figures 465–468

Tingupa arizonica Loomis, 1966, Proc. Biol. Soc. Washington, 79: 228–229, figs. 14–16, ♂.

Types. Male holotype from Mt. Lemmon (8,000 ft.), Santa Catalina Mts., Pima Co., Arizona, in USNM, not seen.

Discussion. I have studied, and illustrate here (Figs. 465–467), males from the type locality collected by J. A. Beatty, 12 November 1960. Loomis (1966) briefly described the nonsexual characters of the species and gave two illustrations of the gonopods. They serve to identify the species as a *Tingupa,* but are otherwise too sketchy to be useful. Loomis did not observe the joint between the basal and second segments of the posterior gonopods; thus his reference to the rudimentary third segment is actually to the fourth segment, which may indeed only be a reduced claw.

Tingupa pallida Loomis
Figures 469–472

Tingupa pallida Loomis, 1939, Bull. Mus. Comp. Zool., 86: 185, figs. 12a–12c, ♂; 1943, Bull. Mus. Comp. Zool., 92: 387, fig. 7, ♂; Shear, 1969, Psyche, 76: 141, Fig. 9, ♂.

Types. Male holotype from River Cave, Hahatunka, Camden Co., Missouri, in MCZ, examined.

Discussion. This species is common in caves in Missouri and Illinois, and has been reported once (Causey, 1951b) from leaf litter, at Collinsville, Illinois. It is colorless and the number and size of the ocelli are reduced. The gonopods (Figs. 469–472) show some differences from the two western species, and the males have 30 segments. A complete description of the nonsexual characters and details of the distribution are given by Loomis (1939, 1943).

Family BRANNERIIDAE Cook

Branneriidae Cook, 1896, Brandtia, 2: 8.

Type genus. Branneria Bollman, 1893.

Diagnosis. The only North American chordeumid with 26 segments.

Description. Twenty-six segments. Mentum divided. Head wider than collum. Antennae short, markedly clavate (Fig. 473). Postcollum segments with thick paranotal swellings (Fig. 474) similar to some species of *Pseudotremia;* dorsum with heavy rugae. Pregonopodal legs of male unmodified. Anterior gonopods: complex, coxae enveloping basal region of telopodite, colpocoxites fused mesally, sharply elbowed. Telopodite (?) with 2 branches, 1 flagelliform. Posterior gonopods: sternum broad, excavate. Coxae flattened, lobed. Telopodite with 2 articles. Tenth legs with coxae enlarged, folded, with glands. Telopodite reduced, 2-segmented. Twelfth sternum and legs normal.

Discussion. Branneria carinata (Bollman) is the only known species. No original descriptive material on this species has been published since 1895, when Cook and Collins treated it briefly in their monograph. The original description (Bollman, 1888) contains little concrete information, and the gonopods have never been illustrated. The relationships of this minute, humicolous form are equally obscure, though it is clearly related to the Tingupidae. The gonopods are so tiny and transparent that they must be mounted on a microscope slide and observed under a phase contrast microscope; even then, it is difficult to distinguish the various regions. Probably many of the peculiarities of *B. carinata* are adaptations to small size, and to living in crevices in the soil. I present below for the first time a detailed description of the gonopods.

Genus *Branneria* Bollman

Branneria Bollman, 1893, U. S. Nat. Mus. Bull., 46: 158.

Type species. Craspedosoma carinata Bollman, by monotypy. The gender of the generic name is feminine.

Branneria carinata (Bollman)

Figures 473–478

Craspedosoma carinatum Bollman, 1888, Ann. New York Acad. Sci., 10: 108.

Branneria carinata, Cook and Collins, 1895, Ann. New York Acad. Sci., 9: 33–34, fig. 1, ♂.

Types. Syntypes from Beaver Creek, Jefferson Co., Tenn., about 2 mi. NE of Strawberry Plains, Tenn.; syntypes deposited in USNM, could not be located.

Description. Male from Torreya Park, Fla.; length, 4.2 mm, width, 0.35 mm. Ocelli 9 on both sides, in 2 irregular rows plus single ocellus. Head rounded (Fig. 473), subspherical, antennae short, clavate, third segment longest, fifth segment widest. Midbody segments (Fig. 474) as described for family. Epiproct rugose and shallowly emarginate. Head dark purplish brown, with irregular lighter markings, antennae lighter, body segments yellowish white, marked purplish brown as shown in Figure 474. Pregonopodal legs not modified, but coxae of seventh legs slightly enlarged and rugose on posterior surface. Anterior gonopods: in anterior view (Fig. 475), sternum bandlike, weak. Coxae subglobose at base, colpocoxites elbowed, truncate; 5 setae in lateral group, 3 in mesal group, strong single seta near apex of each colpocoxite. In posterior view (Fig. 476), telopodites with flagelliform basal branch curving between apical branch of telopodite and colpocoxite, crossing in front of coxae (Fig. 475). Distal telopodite branch longer than colpocoxites, truncate, with prominent knobby projection midway in its length. Acuminate median structure possibly derived from fusion of telopodites basally (see discussion of gonopods of *Pseudotremia,* Cleidogonidae). Posterior gonopods: 3-segmented (Fig. 477); sternum broad, strong, excavated. Distal segment subglobular. Tenth legs (Fig. 478) with enlarged, lobed coxae with glands, telopodite 2-segmented. Eleventh legs with coxae slightly enlarged, shallowly excavated on anterior face (gland remnant?).

Discussion. My study is based on literally hundreds of individuals, about half of them mature males, collected in Florida by Dr. Stewart Peck in Berlese samples of logs and leaf litter. A series of 20 males from this collection ranged in length from 3.95 to 4.26 mm, averaging 4.11 ± 0.12 mm. Ocelli number in this same series varied from seven to ten on each side of the head, with nine the most common number. With the exception of the type locality and the Florida specimens, all the records listed below are based on material kindly loaned by Dr. N. B. Causey. I give these records (see also Map 16) to establish the range of the species.

Records. ALABAMA: *Franklin Co.*, The Dismals; *Talladega Co.*, Sylacauga; *Mobile Co.*, Mobile; *Blount Co.*, near Bangor Cave; *Marshall Co.*, near Guffey Cave. FLORIDA: *Jackson Co.*, Florida Caverns State Park, Marianna; *Liberty Co.*, Torreya State Park, Bristol. GEORGIA: *Rabun Co.*, Mountain City. MISSISSIPPI: *Forrest Co.*; *Wayne Co.*, bank of Buckatunna Riv. on Hwy. 84. NORTH CAROLINA: *Transylvania Co.*, Brevard; *Macon Co.*, Cullasaja Riv. gorge.

Superfamily HETEROCHORDEUMATOIDEA Pocock, NEW STATUS

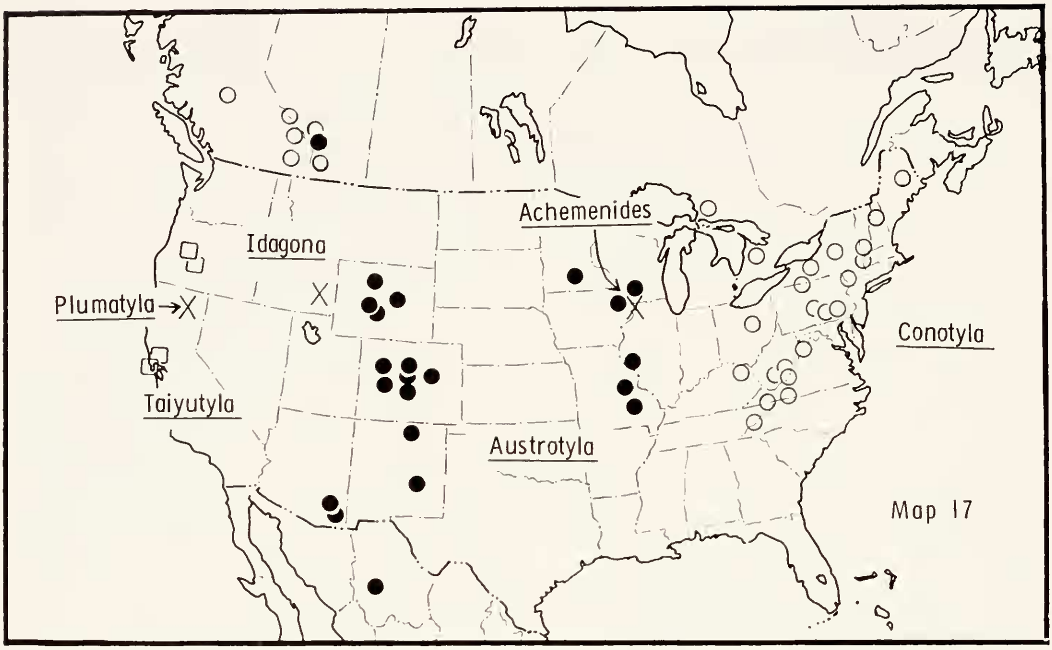
Chordeumid millipeds with 28–32 segments; mentum not divided. Anterior gonopods of various forms: blunt, leglike, 4–5-segmented (Heterochordeumatidae); single segment free from sternite (Conotylidae, Diplomaragnidae, probably Metapidiotrichidae); or a cheirite, formed from complete fusion of gonopod, sternite, and tracheal apodeme (Adritylidae). Posterior gonopods with more or less complex colpocoxites that function in spermatophore transfer, telopodite 2-segmented, or rarely absent (*Idagona*, Conotylidae). Coxal sacs on legs 10 only. Circum-Pacific in distribution.

Included families. Conotylidae Cook, 1896; Adritylidae Shear, 1970; Diplomaragnidae Attems, 1907; Heterochordeumatidae Pocock, 1894; Metapidiotrichidae Attems, 1907; Japanosomidae Verhoeff, 1926.

Discussion. This group of families clearly presents a monophyletic line, one of the few such groups in the Diplopoda whose common descent cannot be doubted. Included are the Heterochordeumatidae, considered by Hoffman (1963) as the most primitive of all chordeumids, and the Adritylidae, one of the most highly specialized North American families (Causey, 1961; Shear, 1971a). I have not studied specimens of the Asian families Heterochordeumatidae, Diplomaragnidae, and Metapidiotrichidae, but it seems that they establish, with the North American Conotylidae and Adritylidae, an easily-delimited group.

The Heterochordeumatidae (Hoffman, 1963) are a supposedly primitive group. They have 32 segments, and occur in Burma and Sumatra. The anterior gonopods are more leglike than in any other chordeumids, being cylindrical and with four to five definite segments. It is unlikely that they play any role in spermatophore transfer. The posterior gonopods are like those of *Adrityla;* the colpocoxite is divided into two unequal branches. But there are also specialized characters: the body segments bear broad paranota. They are so broad that Hoffman (1963) doubted if it would be possible to tell a headless female heterochordeumatid from a platydesmid! Also, the telopodites of the tenth legs are reduced, as in *Adrityla.* Hoffman speculated that *Heterochordeuma* may represent an early offshoot from a common platydesmid-chordeumid ancestor.

The Diplomaragnidae are found in eastern Siberia, Korea (*Diplomaragna*), and Japan (*Syntelopodeuma*). Species have been described by Attems (1898) and by Verhoeff (1914, 1936). These forms also have 32 segments. In *Diplomaragna terricolor* (Attems) (Attems, 1898) and *Synte-*



Map 17. United States, showing distribution of the genera of the family Conotylidae. Dots, *Austrotyla;* circles, *Conotyla;* squares, *Taiyutyla;* crosses, localities of other genera as indicated.

lopodeuma gracilipes Verhoeff (Verhoeff, 1914) the posterior gonopods are much like those of *Heterochordeuma,* but both anterior gonopods are fused together into a complex structure called a *syntelopodite,* which interlocks with the colpocoxites of the posterior gonopods. The tenth legs are reduced in *Diplomaragna,* and of normal size in *Syntelopodeuma.*

The Metapidiotrichidae are not easy to define. According to Attems (1907) the family includes *Metapidiothrix* (Java), *Eudigona, Apodigona* (Chile), and *Schedotrigona* (New Zealand). *Apodigona* has 30 segments, the others 32 (Silvestri, 1903; Attems, 1907); both *Apodigona* and *Eudigona* have gonopods like those in the North American Conotylidae, and Verhoeff (1914) placed *Eudigona* in that family, though his placement of *Apodigona* in the Trichopetalidae is erroneous. *Metapidiothrix* has segmented anterior gonopods that clasp the colpocoxites of the posterior gonopods in the conotylid manner, and reduced tenth and eleventh legs (Attems, 1907). This family is closest to the Conotylidae, and a detailed study of specimens belonging to this family is urgently needed.

The North American families are treated below in greater detail.

Family CONOTYLIDAE Cook

Conotylidae Cook, 1896, Brandtia, 2: 8; Verhoeff, 1932, Zool. Jahrb. Abt. Syst., 62: 500; Hoffman, 1961, Trans. Amer. Entomol. Soc., 87: 263; Shear, 1971, Bull. Mus. Comp. Zool., 141 (2): 58.

Idagonidae Buckett and Gardner, 1967, Michigan Entomol., 1: 117; Shear, 1969, Psyche, 76: 137. NEW SUBJECTIVE SYNONYMY.

Type genus. Of Conotylidae, *Conotyla* Cook and Collins, 1895; of Idagonidae, *Idagona* Buckett and Gardner, 1967.

Included North American genera. Conotyla, Austrotyla, Taiyutyla, Plumatyla, Achemenides, Idagona.

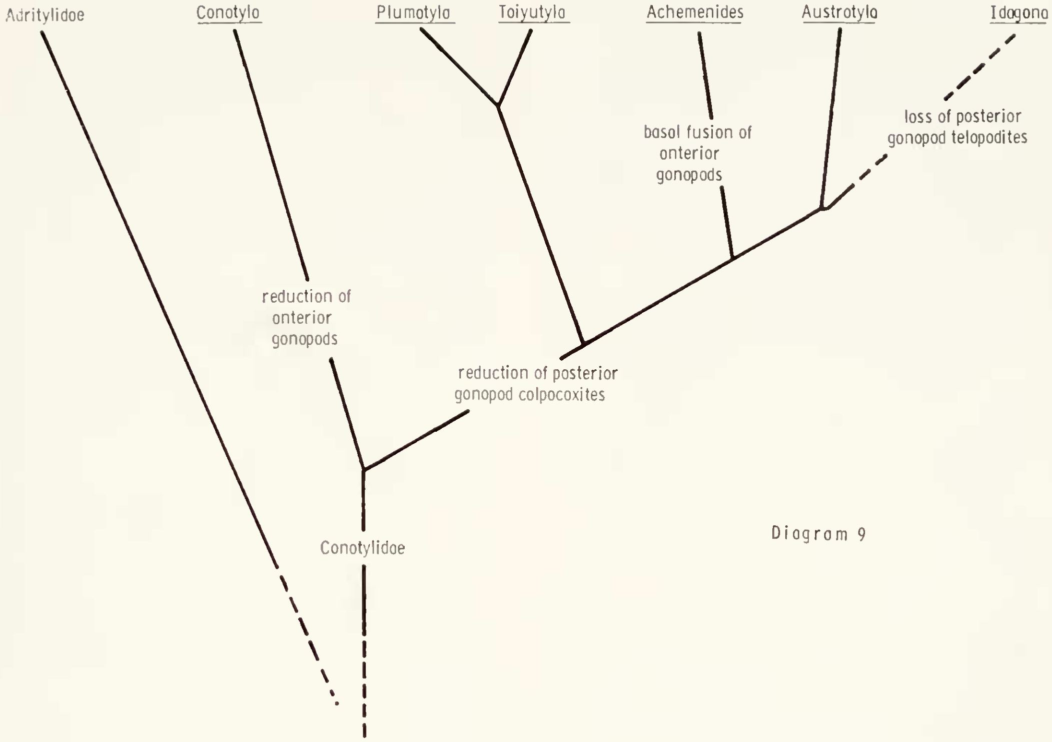


Diagram 9. Hypothetical cladogram of the genera of Conotylidae and the Family Adritylidae. Time scale not to be inferred.

Diagnosis. Distinct from all North American families except Adritylidae in having the mentum not divided, and bearing apparently functional colpocoxites on the posterior gonopods; distinct from the Adritylidae in not having the anterior gonopods fused to their sternites.

Description. Thirty segments. Mentum undivided. Head wider than collum. Antennae long, slender, not clavate. Ocelli always present, usually in a triangular patch, but sometimes reduced in number and size. Postcollum segments with prominent rounded knobs at the bases of the outer segmental setae. Pregonopodal legs of males frequently with modifications, usually consisting of mesal knobs on 1 or 2 segments. Anterior gonopods: single-articled; free from sternites; curving around colpocoxites of posterior gonopods, or flattened, platelike. Posterior gonopods: coxae free from sternites, with prominent sclerotized colpocoxites; telopodites absent (*Idagona*), or 2-segmented, distal article swollen, turned dorsal, both articles without significant muscles. Coxae of tenth legs enlarged, with coxal glands. Coxae and prefemur of eleventh legs sometimes modified, but coxae without glands. Twelfth legs and sternum normal.

Distribution. North America (Map 17) (Japan ?).

Discussion. A more detailed discussion of the biology and gonopod morphology is in my recent revision (Shear, 1971a). The dubious taxonomic status of the generic names *Zygotyla*, *Cookella*, and *Bollmanella* are also discussed there. The relationships of the genera to one another are discussed separately below; a hypothetical cladogram based on this evidence is presented in Diagram 9.

KEY TO GENERA OF CONOTYLIDAE IN NORTH AMERICA

1a. Anterior gonopods much larger than posterior (Figs. 479, 481); telopodites of posterior gonopods absent; Idaho caves .... *Idagona*

1b. Anterior gonopods not larger than posterior (including telopodites); telopodites of posterior gonopods 2-segmented (Fig. 483) 2

2a. Anterior gonopod sternum divided; anterior gonopods fused to each other at base, much larger than colpocoxites of posterior gonopods (Figs. 485, 486); northern Illinois, northeastern Iowa, southwestern Wisconsin .... *Achemenides*

2b. Anterior gonopod sternum not divided; anterior gonopods not fused to each other, though they may be closely appressed (Figs. 487, 492), smaller or larger than colpocoxites of posterior gonopods 3

3a. Anterior gonopods flattened, platelike, often appressed in the midline (Figs. 487, 492), larger than or subequal to colpocoxites of posterior gonopods 4

3b. Anterior gonopods not flattened, often with complex or plumose branches (Figs. 482, 490), smaller than or subequal to colpocoxites of posterior gonopods 5

4a. Anterior gonopod sternum with lateral processes partially fused to lateral sides of gonopods (Fig. 487); gonopods complex on posterior surface (Fig. 488); colpocoxites of posterior gonopods small, cupped anteriad; Illinois and Missouri, and Rocky Mountains from Alberta to Chihuahua .... *Austrotyla*

4b. Anterior gonopod sternum without such processes, heavily sclerotized, completely surrounding bases of gonopods (Fig. 492); colpocoxites of posterior gonopods subequal to anterior gonopods, frequently complex and branched, never cupped anteriad (Fig. 493); Pacific coast from central Oregon to San Francisco Bay region .... *Taiyutyla*

5a. Anterior gonopod sternum with lateral process partially fused to lateral edge of gonopod; gonopod 2-branched, mesal edge of major branch laciniate (Fig. 490); colpocoxite of posterior gonopod 2-branched; caves in northern California and southern Oregon .... *Plumatyla*

5b. Anterior gonopod sternum simple and bandlike (Fig. 482), gonopod with one or two small branches; colpocoxites of posterior gonopods with complex posterior surface, but not 2-branched; eastern North America from Maine to North Carolina, Rocky Mts. of Alberta and British Columbia, Sierra Nevada of California .... *Conotyla*

Genus *Idagona* Buckett and Gardner

Idagona Buckett and Gardner, 1967, Michigan Entomol., 1: 120.

Type species. Idagona westcotti Buckett and Gardner, by monotypy and original designation.

Diagnosis. Distinct from all other Conotylidae in the comparatively greater size of the anterior gonopods and the absence of telopodites from the greatly reduced posterior gonopods. Coxae of legs 10 are enlarged and lobed; those of leg 11 slightly so, but lacking a gland.

Discussion. This genus is the type of the family Idagonidae, described by Buckett and Gardner (1967) at the same time as the genus. In order to make Conotylidae a meaningful family, Idagonidae, with its only included genus, is considered synonymous. *Idagona* falls well within the Conotylidae, though Idagonidae may have to be considered a subfamily when the western conotylids are more completely known. The drawings presented by Buckett and Gardner (1967) are adequate for recognition of the species. However, some of the details of the gonopod structure, in particular the tracheal apodemes, are shown here for the first time. The large anterior gonopods (Figs. 479, 480) are separate from the sternum. The posterior gonopod sternum (Fig. 479) is much reduced, being mainly membranous mesally but well sclerotized around the spiracles. Despite the specializations, which may have resulted in a reversal of the usual functional roles of the gonopods in conotylids, *Idagona* retains some fairly primitive features. The coxal region of the anterior gonopods (Fig. 481) is more clearly set off here than in any other genus of the Conotylidae, and the presence of setae on the anterior gonopod sternum (Fig. 480) may also be primitive.

Idagona is related to the *Austrotyla-Taiyutyla* line within the Conotylidae.

Genus *Conotyla* Cook and Collins

Conotyla Cook and Collins, 1895, Ann. New York Acad. Sci., 9: 70–71; Shear, 1971, Bull. Mus. Comp. Zool., 141(2): 64.

Proconotyla Verhoeff, 1932, Zool. Jahrb. Abt. Syst., 62: 501.

Type species. Of *Conotyla, C. fischeri* Cook and Collins, 1895, by original designation; of *Proconotyla, P. blakei* Verhoeff, 1932, by monotypy.

Diagnosis. Diagnostic characters are given in the above key.

Discussion. My recent revision (Shear, 1971a) has a key to species. In *Conotyla*, the anterior gonopods (Figs. 482, 484) are free from the sternum, but are fused into a single article, usually passing laterad to the colpocoxites of the posterior gonopods in a distinct plumose region. The posterior gonopod telopodites are 2-articled, enlarged, and turned dorsad (Fig. 483). The colpocoxites of the posterior gonopods are variable. In some species they are quite simple and acuminate, while in others they bear a complex of rodlike and plumose branches. There is good evidence in this genus of spermatophore transfer by the colpocoxites of the posterior gonopods, since spermatophores have been found on both the extruded tenth coxal glands and the tips of the colpocoxites. The exact mechanism of transfer is unknown.

Distribution. Conotyla is quite widespread for a milliped genus. The present distribution (Map 17) is probably a relict of an earlier, more continuous distribution. There is a considerable morphological gap between species of the *atrolineata* group in Alberta and British Columbia and the several species groups in the Appalachians. It is interesting that species in the highly dissected Rocky Mountain habitats are more widespread than species in the Appalachians, which are often extremely limited in their distribution. However, the western species all appear to be limited to coniferous forests at high altitudes, and these forests may be more or less continuous for many miles. Possibly the advance and retreat of the Pleistocene glaciers, much more pronounced in the east, divided the Appalachian habitat into small habitable areas, from which the eastern species of *Conotyla* spread to their present distributions. Probably the major part of the speciation process took place when populations were isolated in valleys during glacial maxima and became adapted to low temperatures (Shear, 1971a). Most species of *Conotyla* now occur at higher elevations and are active mainly in late fall and very early spring.

Two species (*Conotyla blakei, C. fischeri*) are common in glaciated territory, *C. blakei* also occurring to the south in caves. *Conotyla blakei* has the widest range of any eastern conotylid, presenting an example of a milliped not much different from many of its congeners but somehow capable of much greater dispersal and successful colonization. It is closely related to *C. bollmani*, a species primarily of caves in Indiana, but is not related to the majority of Appalachian species. *Conotyla fischeri* occurs throughout central New York state, and is closely related to *C. personata* of northern Ohio; both these species are derived from Appalachian forms. At the extreme southern end of the range of the genus in North Carolina and Tennessee, species of *Conotyla* are rare and localized, occurring mostly in coniferous zones on the tops of the highest mountains.

Another factor limiting the distribution of the genus in the southern Appalachians may be competition with many species of *Pseudotremia*, which have a similar niche and are more common.

Genus *Achemenides* Shear

Achemenides Shear, 1971, Bull. Mus. Comp. Zool., 141(2): 84.

Type species. Conotyla pectinata Causey, 1952, by monotypy and original designation.

Diagnosis. Distinct from all other conotylid genera in that the anterior gonopods are joined at the base and drawn out anteriorly into a curved knob; also in having knobs on 2 segments of the last pregonopodal leg.

Discussion. The gonopod anatomy of *A. pectinatus* (Figs. 485, 486) departs somewhat from the usual conotylid pattern. While the anterior gonopods (Fig. 485) are roughly similar to those of *Austrotyla,* as are the reduced colpocoxites of the posterior gonopods (Fig. 486), the anterior sternum is bandlike, as in *Conotyla,* though it is also divided bilaterally. I do not think this division is primitive, but believe it to be a secondary development to accommodate the anterior knob of the basally fused anterior gonopods.

The fusion of the bases of the anterior gonopods recalls *Syntelopodeuma* (Diplomaragnidae) of Japan, but there are no other similarities. I think *Achemenides* has evolved from conotylid stock in North America.

Distribution. The species is known only from caves and mines in the adjacent areas of Illinois, Iowa, and Wisconsin. I have earlier speculated (1971a) that the troglophilic habit of the species may be due to the climatic severity of the Wisconsinian glaciation. The area in which the species occurs is the so-called driftless area, an area assumed to have been free of ice and in which species may have survived the glaciation in caves (see Frye, 1965; Cushing, 1965, for a more complete discussion). The glaciers would have wiped out surface populations of the driftless area by lowering beyond their tolerance the minimum annual temperature. Cave temperatures, however, generally approximate the local average temperature the year 'round. Thus a cold-adapted animal could survive such conditions in caves.

Genus *Taiyutyla* Chamberlin

Taiyutyla Chamberlin, 1952, Nat. Hist. Misc. Chicago Acad. Sci., No. 113: 1; Shear, 1971, Bull. Mus. Comp. Zool., 141(2): 86.

Type species. Taiyutyla corvallis Chamberlin, 1952, by original designation.

Diagnosis. The characters given in the key serve to diagnose this genus, particularly the size and shape of the colpocoxites (Fig. 493), which are similar to those of *Conotyla,* while the anterior gonopods (Fig. 492) are similar to those of *Austrotyla.* My revision (Shear, 1971a) has a key to the described species.

Discussion. Little can be said about this genus. Only a few specimens of mature males are known, probably owing to a lack of suitable collecting methods in the Coast Ranges of the Pacific Northwest, where the three known species occur. *T. francisca* was collected in pine duff. There are doubtless many undescribed species.

Genus *Austrotyla* Causey

Austrotyla Causey, 1961, Proc. Biol. Soc. Washington, 74: 260; Shear, 1971, Bull. Mus. Comp. Zool., 141(2): 89.

Type species. Conotyla specus Loomis, 1939, by original designation.

Diagnosis. In addition to the characters given in the key, all species have the male pregonopodal legs modified the same way: femoral knobs on legs 3 and 4. In some of the species, anterior knobs appear on the coxae of legs 10 and 11. Shear (1971a) has a key to described species.

Discussion. This large, primarily western genus forms a compact group with *Taiyutyla* and *Plumatyla,* and it is likely that they are actually closely related. The gonopods differ considerably from those of *Conotyla.* In *Austrotyla,* the anterior gonopods are much larger than the colpocoxites of the posterior gonopods (Figs. 487, 488) and are platelike and contiguous in the midline. The colpocoxites of the posterior gonopods are small and inconspicuous (Fig. 77). This structural reversal may be evidence that the functional roles of the gonopods are reversed in this genus, and in *Achemenides* and *Idagona.* The mating of living *Austrotyla* has not been studied. Within the genus, species are remarkably similar, considering the great geographical separation between them. *Austrotyla borealis*, of the Rocky Mountains of Alberta, is quite similar to *A. specus* of Missouri and Illinois; *A. coloradensis* (Colorado) is very close to *A. chihuahua* (Chihuahua, Mexico).

Distribution. The genus is primarily a Rocky Mountain group, with isolated species in caves and a few surface localities in Missouri and Illinois. There are other such distributions known for soil-dwelling arthropods: the spider genus *Atypoides* (Coyle, 1968) and the milliped family Nearctodesmidae (Hoffman, 1962) are good examples. Such distributions are relicts of previously more continuous ones, and it seems possible that when the droughts of the Pliocene brought the Great Plains into being, large areas became inhospitable to conotylids and divided *Austrotyla's* range. Glacial advance and retreat during the Pleistocene can perhaps be used to explain in part the cave populations of *A. specus*.

In the Rocky Mountains, species of *Austrotyla* are quite boreal in habitat. Extensive collections by H. W. Levi of *A. coloradensis* are mostly from forests about 7000 ft. (2500 m) in elevation; the most southerly species, *A. chihuahua*, is from the Sierra Madre Occidental, at an elevation of 6500–7000 ft. (2250–2500 m).

Genus *Plumatyla* Shear

Plumatyla Shear, 1971, Bull. Mus. Comp. Zool., 141(2): 94.

Type species. Conotyla humerosa Loomis, 1943, by monotypy and original designation.

Diagnosis. Besides the distinctive gonopods mentioned in the key, *P. humerosa* is without pigment and has reduced, irregularly arranged ocelli (about 10); no other conotylid is as strongly modified for cave life.

Discussion. The gonopods (Figs. 490, 491) show certain intermediate characters between those of *Taiyutyla* and *Austrotyla*, and may be similar to a possible common ancestor of these two genera. Little else can be said, owing, as usual, to a lack of mature specimens. It would be remarkable if this were the only species to occur throughout the lava flow regions of northern California; we might expect additional species in other neighboring caves.

Family ADRITYLIDAE Shear

Adritylidae Shear, 1971, Bull. Mus. Comp. Zool., 141(2): 57.

Type genus. Adrityla Causey, 1961. The family contains only one genus with a single species, *Conotyla deseretae* Chamberlin, 1910.

Diagnosis. Adrityla deseretae, Figures 494–496, is the only North American species with the anterior gonopods each of a single piece, formed from a fusion of the gonopod, with its sternite, and the tracheal apodeme. The coxae of the posterior gonopods and tenth legs are also fused to their respective sterna. This is also the largest (*ca.* 25–30 mm) North American species.

Description. Thirty segments. Mentum undivided. Head wider than collum. Antennae long, slender, not clavate. Ocelli in a triangular patch. Pregonopodal legs with femoral knobs. Anterior gonopods: 1-segmented, fused with sternites and tracheal apodemes (Fig. 494). Posterior gonopods: colpocoxite divided into two branches, telopodite 2-segmented (Fig. 495). Coxae of tenth legs enlarged, lobed, with gland, telopodites much reduced (Fig. 496). Coxae of eleventh legs without coxal glands. Twelfth legs and sternum normal.

Distribution. The single known species of this family is found in the Wasatch Mts. of northeastern Utah, where it is common in canyons. F. A. Coyle collected specimens near Timpanogos Cave National Monument at about 7000 ft. elevation, in ponderosa pine parkland on canyon slopes (Coyle, personal communication). There may be other species in the Rocky Mts. to the north and south, but these mountains have been very poorly collected.

Discussion. While highly specialized, the anterior gonopods are derived from a conotylidlike form. As in *Achemenides* (Conotylidae), the divided sternum is probably not primitive. The large colpocoxites might indicate that this family began to diverge from the basic conotylid stock before the reduction of colpocoxites that gave rise to the *Austrotyla* line. The reduction of the telopodites of leg 10 is undoubtedly parallel evolution with some of the Asian genera of the superfamily, rather than a primitive condition.

Superfamily CLEIDOGONOIDEA Cook, NEW STATUS

Chordeumid millipeds with 28 or 30 segments; mentum divided. Anterior gonopods with prominent colpocoxites sometimes divided into two branches, but always lacking flagella. Telopodites fused at their bases (Cleidogonidae) or free (most Trichopetalidae), sometimes with accessory laciniate branches (Trichopetalidae), not fused to coxae. Posterior gonopods with sternum narrow, sometimes with processes; coxae of posterior gonopods lacking colpocoxites, but often with lobes or knobs; telopodites reduced, 4- to 1-segmented. Coxae of legs 10 and 11 with glands. Panama to Newfoundland.

Included families. Cleidogonidae Cook 1895; Trichopetalidae Verhoeff 1932.

Discussion. For many years, taxonomists assumed a relationship between the Trichopetalidae and Conotylidae (Cook, 1895; Causey, 1960a; Hoffman, 1961; Shear, 1971a), based mainly on the similarity in body form and the reduction of the posterior gonopods. A thorough study of the gonopods and other characters reveals, however, that the family Trichopetalidae is very close to the Cleidogonidae; species of *Mexiterpes* (Trichopetalidae) combine features of both families. Cleidogonidae are predominantly an austral group, while the Trichopetalidae are boreal in distribution, occurring well into glaciated territory, on high mountains and in caves.

This superfamily seems to be exclusively North American and not closley related to any other chordeumid group.

Family CLEIDOGONIDAE Cook

The preceding detailed revision of the Cleidogonidae furnishes all the necessary information on this family.

Family TRICHOPETALIDAE Verhoeff

Trichopetalidae Verhoeff, 1932, Zool. Jahrb. Abt. Syst., 62: 485; Hoffman, 1961, Trans. Amer. Ent. Soc., 87: 262; Causey, 1963, Psyche, 70: 237 (key to genera).

Type genus. Trichopetalum Harger, 1872.

Diagnosis. Distinct from the Cleidogonidae in having extremely long segmental setae, the telopodites of the anterior gonopods not fused (except in *Mexiterpes*) and with an anterior laciniate branch or area. In all cleidogonid genera except *Tiganogona,* the posterior gonopods are 4- to 6-segmented, while in the species of Trichopetalidae, they are 2- or 3-segmented. Only a few Mexican species of Cleidogonidae have the prominent paranota found in all trichopetalids.

Description. Twenty-eight or 30 segments. Mentum divided, but often hard to see because of weak sclerotization. Ocelli few or absent; if present arranged in single row or lunate patch. Trunk segments with prominent paranota and long, strong segmental setae, often with mucous droplets. Anterior gonopods: sternum broad, sclerotized, often expanded in front for muscle attachment. Coxae distinct, but sometimes fused to each other in midline, with 1- to 3-branched colpocoxites of various forms, setose. Telopodite 1-segmented, usually lobelike, not fused to coxae, usually not fused to one another (except in *Mexiterpes*), with anterior plumose branch or area. Posterior gonopods: sternum weakly sclerotized, gonopod coxae usually widely separated, musculature weak, coxae usually without lobes or processes; telopodites 1- or 2-segmented, additional segments some-

Map 18. North America, showing distribution of genera of the family Trichopetalidae. Dots, *Trigenotyla* (as indicated), and *Trichopetalum*; circles, *Scoterpes* and (as indicated) *Mexiterpes*.

times indicated by vague sutures, with or without claw. Coxae of legs 10 and 11 with coxal glands, slightly enlarged. Females lacking postgenital plate.

Included genera. Trichopetalum, Scoterpes, Mexiterpes, Trigenotyla.

Distribution (Map 18). Georgia west to Missouri, north to Newfoundland; British Columbia? Colorado? Caves in San Luis Potosí and Querétaro, Mexico.

Discussion. The form of the gonopods, the divided mentum, and the presence of coxal glands on legs 10 and 11 ally this family to the Family Cleidogonidae. In addition, *Mexiterpes metallicus* (new species, described below) has several characters in common with *Pseudotremia* spp.; the anterior gonopod telopodites are basally fused and are not lobelike, and there are median structures developed from this fused base. Like the Cleidogonidae, this family probably had its origin in the Mexican highlands and spread north, differentiating into two major stocks from a proto-*Mexiterpes* ancestor. The most successful of these is represented by *Tricho-*

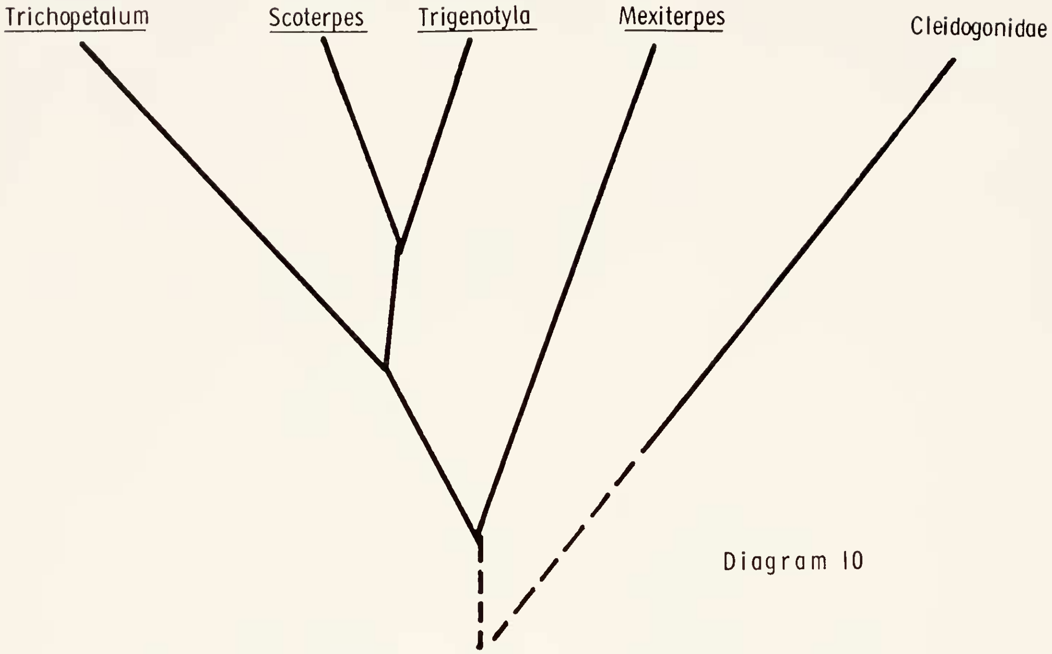


Diagram 10. Hypothetical cladogram of genera of Trichopetalidae, showing relationship to the family Cleidagonidae (compare Diagram 1). Time scale not to be inferred.

petalum, a widespread genus occurring in most of eastern North America inland of the Fall Line on the Atlantic Piedmont. A second stock is represented by two genera; *Trigenotyla,* an Ozarkian relict, and *Scoterpes,* now limited to Appalachian and Ozark caves. The two species of *Mexiterpes* occurring in Mexican caves are apparently the most primitive trichopetalids, but are also quite specialized in their resemblance to cleidogonids. A hypothetical cladogram is presented in Diagram 10. The group is badly in need of revisionary studies at the generic level, as the extensive synonymies presented below indicate.

KEY TO GENERA OF TRICHOPETALIDAE, BASED ON MALES

1a. Anterior gonopod telopodites basally fused, not lobelike, decurved dorsad (Fig. 537); San Luis Potosí, Querétaro, in caves .... *Mexiterpes*

1b. Anterior gonopod telopodites not fused, lobelike (Figs. 523, 503) 2

2a. Laciniate branch of anterior gonopod with base visible in posterior view, not concealed by body of telopodite (Figs. 523, 528); colpocoxites with two or three branches 3

2b. Laciniate branch of anterior gonopod with base concealed in posterior view (Figs. 500, 503); colpocoxites with one or two branches, often with an anterior patch of small scales .... *Trichopetalum*

3a. Pigmented, with ocelli; northwestern Arkansas .... *Trigenotyla*

3b. Not pigmented, ocelli absent; caves in Illinois, Missouri, and Appalachian region from Kentucky to Alabama and Georgia .... *Scoterpes*

Genus *Trichopetalum* Harger

Trichopetalum Harger, 1872, Amer. J. Arts Sci., 4: 117; Cook and Collins, 1895, Ann. New York Acad. Sci., 9: 62; Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull., 212: 102 (list of species); Causey, 1967, Proc. Biol. Soc. Washington, 80: 117 (key to species).

Zygonopus Ryder, 1881, Proc. U. S. Nat. Mus., 3: 527; Cook and Collins, 1895, Ann. New York Acad. Sci., 9: 59; Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull., 212: 103

(list of species); Causey, 1960, J. New York Entomol. Soc., 67: 70 (key to species). NEW SUBJECTIVE SYNONYMY.

Tynopus Chamberlin, 1940, Canadian Entomol., 72: 57. NEW SUBJECTIVE SYNONYMY.

Flagellopetalum Causey, 1951, Proc. Biol. Soc. Washington, 64: 119; Loomis, 1966, Proc. Biol. Soc. Washington, 79: 229. NEW SUBJECTIVE SYNONYMY.

Types. Of *Trichopetalum*, *T. lunatum* Harger, by subsequent designation of Cook and Collins, 1895; of *Zygonopus*, *Z. whitei* Ryder by monotypy; of *Tynopus*, *T. dux* Chamberlin by monotypy; of *Flagellopetalum*, *F. stannardi* Causey, by monotypy.

Notes on synonymy. The synonymies given above will doubtless prove controversial. However, when segment number and troglobitic adaptations are not considered to be, by themselves, clear evidence of generic groupings, the species included in the genera listed above form a natural group. Careful comparison of the gonopod illustrations presented here will confirm this. *Zygonopus* has been separated from *Trichopetalum* on the basis of a higher segment number, troglobitic adaptations, and pregonopodal leg modifications. But as I have pointed out above, in the section on characters, reduced segment number is an adaptation to small size and not a taxonomic character of great importance. *Trichopetalum syntheticum* (new species, described below) has 28 segments and is eyeless and depigmented. Pregonopodal leg modifications vary within genera, see description of *Scoterpes ventus* below. *Tynopus dux* is a typical species of *Trichopetalum*, as Hoffman (1961) suggested. Unfortunately, the types of *Flagellopetalum stannardi* Causey and *F. quadratum* Loomis are not available for study and are the only known material of the genus. The museums where they were to have been deposited (Illinois Nat. Hist. Surv. and USNM, respectively) have no record of ever having received them. However, from the information presented in the descriptions of these two species, I do not hesitate to synonymize the genus under *Trichopetalum*.

Diagnosis. Most epigean members of the genus have 28 segments; *Trigenotyla parca* has 30. Troglobitic species may be separated from *Scoterpes* by a comparison of the figures of the gonopods given below.

I have examined and here illustrate the following species of *Trichopetalum*.

Trichopetalum lunatum Harger
Figures 497–499

Trichopetalum lunatum Harger, 1872, Amer. J. Arts Sci., 4: 118. Causey, 1967, Proc. Biol. Soc. Washington, 80: fig. 1, ♂.

Trichopetalum album Cook and Collins, 1895, Ann. New York Acad. Sci., 9: 64, figs. 22–29, 36–45, ♂.

Types. Male holotype of *T. lunatum* from New Haven, Connecticut, whereabouts unknown; of *T. album*, from Syracuse, Onondaga Co., New York, in USNM, not examined.

Notes. Causey (1967) reports this species from Pennsylvania, Wisconsin, New York, and Connecticut. I have collected it in West Virginia: Palmén (1952) reported it as fairly common in Newfoundland. Specimens labelled as being from the Pinnacle Mountains of British Columbia are in the MCZ. Figure 497 is based on material from the Connecticut Lakes region of northern New Hampshire. Variation is concentrated in the form of the tip of the colpocoxite (West Virginia specimen, Fig. 499; British Columbia (?) specimen, Fig. 498).

Trichopetalum uncum Cook and Collins
Figures 500, 501

Trichopetalum uncum Cook and Collins, 1895, J. New York Acad. Sci., 9: 66, fig. 51, ♂; Causey, 1967, Proc. Biol. Soc. Washington, 80: 119 (records).

Types. Male holotype from Bloomington, Monroe Co., Indiana, reported to be in USNM, not examined.

Notes. Chamberlin and Hoffman (1958) give the distribution as "Indiana and Illinois, south to Arkansas." Causey (1967) has recently recorded it from Missouri, Oklahoma, and Kentucky. My illustrations (Figs. 500, 501) are based on material from a cave in Stone County, Missouri. Some of the individuals in this collection lacked ocelli, while others had only four poorly pigmented ones.

Trichopetalum dux (Chamberlin)
NEW COMBINATION
Figures 502–504

Tynopus dux Chamberlin, Canadian Entomol., 72: 57.

Types. Male holotype collected in Duke Forest, Durham Co., North Carolina, 10 December, 1939 by N. B. Causey, in R. V. Chamberlin collection, University of Utah, Salt Lake City, Utah; examined.

Notes. The male holotype is about 4.5 mm long, has five ocelli in a single curved row with a single ocellus just below the center of the row. The pregonopodal legs are enlarged and crassate. The gonopods have never been illustrated, and are shown in Figures 502–504. The anterior gonopods resemble those of *T. uncum* in some details, but the colpocoxites are smaller, and the telopodites have a definite apical lamella not present in *T. uncum.*

Trichopetalum syntheticum n. sp.
Figures 505–510

Types. Male holotype and two immature specimens from Crossings Cave, 1.5 miles north of Paint Rock, Jackson Co., Alabama, collected 23 December 1967 by W. Torode. The specific epithet, a Latin adjective, refers to the combination of characters in this species previously considered of generic importance in separating *Trichopetalum* and *Zygonopus.*

Diagnosis. Not closely related to other species of *Trichopetalum*, except possibly *T. subterraneum.* The short coxites and concealed plumose branch of the telopodite are distinctive.

Description of male holotype. Length, 5.5 mm. Twenty-eight segments. Segmental setae long, as in *Scoterpes.* Ocelli absent, body unpigmented. Pregonopodal legs unmodified. Anterior gonopods (Figs. 507–509) simplified; sternum as in *T. cornutum*, but lacking swollen frontal areas. Coxae subglobular, meeting in midline along most of their length, mesal group of three setae near base, lateral setae group diffuse over anterior surface; coxite short, thin, truncate, about one-third length of coxa. Telopodites large, basally depressed, roughly triangular in posterior view; laciniate branch hidden on anterobasal surface. Posterior gonopods (Fig. 510) typical, 3-articled, without a claw.

Notes. This species greatly resembles a small *Scoterpes*, but has 28 segments and materially different gonopods. The antennae (Fig. 505) are short; compare Figures 525 and 531. The gonopods lack the swollen areas usually found in *Trichopetalum*, but the species is obviously a troglobite, and this may be a reduced character.

Trichopetalum cornutum Cook and Collins
Figures 511–513

Trichopetalum cornutum Cook and Collins, 1895, Ann. New York Acad. Soc., 9: 66, figs. 46–49, ♂.

Types. Male holotype from Bloomington, Indiana, in USNM, not examined.

Notes. Causey (1967) examined specimens from Indiana, Michigan, Kentucky, and Tennessee. Figures 511–513 are based on material from Highlands, Macon Co., North Carolina, collected from a Berlese sample of *Rhododendron* litter.

Trichopetalum packardi (Causey)
NEW COMBINATION
Figures 514, 515

Zygonopus packardi Causey, 1960, J. New York Entomol. Soc., 68: 77–79, figs. 8, 9, ♂.

Types. Male holotype and female paratype from Luray Cave, Page Co., Virginia, deposited in the American Museum of Natural History, not examined.

Notes. Figures 513 and 514 were drawn from specimens collected by John Holsinger in Slussers Chapel Cave, Montgomery Co., Virginia. Comparison with the preceding figures of species traditionally placed in the genus *Trichopetalum* should prove convincing as regards the synonymy of *Zygonopus* with that genus. All of the species previously assigned to *Zygonopus* are troglobites from the adjacent regions of Virginia and West Virginia.

Genus *Scoterpes* Cope

Scoterpes Cope, 1872, Amer. Nat., 6: 414; Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull., 212: 101 (list of species).

Type species. Spirostrephon copei Packard, by original designation.

Diagnosis. Can be confused with 30-segmented troglobitic members of *Trichopetalum*, but the gonopods are very different in form; the colpocoxites bear a roughly T-shaped apical branch (Fig. 518). Species of *Scoterpes* are nowhere sympatric with 30-segmented troglobitic species of *Trichopetalum*.

Notes. Species of this exclusively troglobitic genus are known from caves in Kentucky, Tennessee, Alabama, Georgia, Missouri, and Illinois. When all species are described, the total number may rise to 30. *Scoterpes* is closely related to *Trigenotyla*, and the two genera may someday have to be combined. This fact, and the distribution of S. *dendropus* in Missouri and Illinois, indicates that *Scoterpes* is a more primitive genus than the possibly derived *Trichopetalum*, and not the reverse, as Causey has suggested (Causey, 1967). The Appalachian species seem to be divisible into at least two species groups, one including species similar to S. *austrinus* Loomis, with simple, T-shaped colpocoxites, and another group near S. *copei* and S. *ventus* (new species, described below) resembling S. *dendropus* of Missouri in the more complex, branched colpocoxites. As with most chordeumid genera, a thorough revision is badly needed, particularly considering the large number of undescribed taxa. I examined, and illustrate, the following species:

Scoterpes copei (Packard)
Figures 516, 517

Spirostrephon (*Pseudotremia*) *copei* Packard, 1871, Amer. Nat., 5: 748.
Scoterpes copei, Cook and Collins, 1895, Ann. New York Acad. Sci., 9: 55, figs. 12, 13, ♂.

Types. Male paratype from Poynter's Cave in Mammoth Cave region, Edmonson Co., Kentucky, in MCZ, examined.

Notes. Chamberlin and Hoffman (1958) are certainly in error when they give the range of this species as extending south from the type locality to Georgia. *Scoterpes copei* has gonopods (Figs. 516, 517) intermediate in complexity between those of S. *dendropus* and S. *austrinus* (Fig. 519).

Scoterpes austrinus Loomis
Figures 518–520

Scoterpes austrinus Loomis, 1943, Bull. Mus. Comp. Zool., 92: 386, fig. 6, pl. 1, figs. 1, 2, ♂.

Types. Male holotype from Manitou Cave, 1 mi. south of Fort Payne, De Kalb Co., Alabama, in MCZ, examined.

Notes. Chamberlin (1946) described a subspecies, S. *austrinus nudus*, which he claimed differed in lacking a claw on the posterior gonopods. Individuals from the same cave often differ in this character, so I do not think that it is of any importance; the question is whether or not S. *austrinus nudus* is a separate species or a synonym of S. *austrinus*. I have not examined the types of *nudus*. The illustrations presented here (Figs. 519–520) of S. *austrinus* are of material from White River Cave, Floyd County, Georgia, which I compared with the holotype.

Scoterpes ventus n. sp.
Figures 521–526

Types. Male holotype and paratype from Blowing Cave, Sequatchie, Marion Co., Tennessee, collected 29 August 1968 by S. B. Peck. The specific epithet is a Latin noun in apposition, "wind," and refers to the name of the type locality.

Diagnosis. Close to *S. copei* and *S. dendropus.* Distinct from *S. dendropus* in the modification of legpair 6, and from *S. copei* in the much greater complexity of the anterior gonopod coxae.

Description of male holotype. Length, 10 mm. Ocelli absent. Legs 3–7 of male much enlarged, crassate, legs 6 and 7 longer than legs 3–5; leg 6 (Fig. 525) with fourth article swollen, irregular knob at mesobasal side; leg 7 somewhat more slender than leg 6, longer. Anterior gonopods (Figs. 521–523) similar to those of *S. dendropus,* with lateral and medial setae groups, depressed. Coxites 3; lateral coxites short, rounded, with crown of chitinous hooks solidly fused to coxite, not with sockets. Middle coxite the longest, slightly sinuous, with irregular bumps on apical fourth. Mesal coxite simple, acuminate. Telopodites complexly lobed, large laciniate branch proximad of apex. Posterior gonopods (Fig. 524) simple, 2-articled, with small knob (pointed like claw in paratype), setose.

Notes. Causey (1960a) separated *Zygonopus* from *Scoterpes* on the basis of the enlarged and bowed sixth leg of *Zygonopus* contrasted with the unmodified pregonopodal legs of *Scoterpes.* Causey's statements must have been based on *S. dendropus,* since Loomis (1939) illustrates the crassate sixth leg of *S. copei.* There is considerable variation in pregonopodal leg modifications in *Scoterpes,* and thus it is not a reliable diagnostic character.

Genus *Trigenotyla* Causey

Trigenotyla Causey, 1951, Proc. Biol. Soc. Washington, 64: 118.

Type species. Trigenotyla parca Causey, by monotypy.

Diagnosis. Differs from all other 30-segmented epigean trichopetalids in the very large laciniate portion of the anterior gonopod telopodite.

Notes. Trigenotyla is clearly related to *Scoterpes,* and may at some future time be placed as a synonym of *Scoterpes,* but more must be found out about *Scoterpes* species first. Though not a troglobite, *T. parca* is frequently found in caves in Arkansas. The strong, swordlike setae on the anterior face of the anterior gonopod colpocoxite (Fig. 527) are unusual, as are the large telopodites (Fig. 528). The posterior gonopod coxae are prolonged beyond the insertion of the telopodite segment. The specimen illustrated here was collected in Granny Dean Cave, 10 mi. southeast of Fayetteville, Washington County, Arkansas, by S. B. Peck, 9 June 1969.

Genus *Mexiterpes* Causey

Mexiterpes Causey, 1963, Psyche, 70: 235.

Type species. Mexiterpes sabinus Causey, by monotypy.

Diagnosis. The fused telopodites of the posterior gonopods, which are not lobelike and lack a laciniate or plumose branch, distinguish this genus from other trichopetalids.

Notes. This genus links the family Trichopetalidae with the family Cleidogonidae. The gonopods of *Mexiterpes metallicus* closely resemble those of *Pseudotremia* species (Cleidogonidae); even if this resemblance is due to convergent evolution, the basic morphology of the gonopods is quite similar: the large, curved colpocoxites, fused telopodites and median structures derived from the fused telopodite bases. The body form and posterior gonopods are typical of trichopetalids, however. In the original generic diagnosis, Causey (1963b) stated that the genus contains only eyeless species. This is true of the type species, *M. sabinus,* but *M. metallicus* has a few poorly pigmented ocelli. The posterior gonopods of *M. metallicus* also differ somewhat from those illustrated by Causey for *M. sabinus,* but see below.

Mexiterpes sabinus Causey
Figures 529–531

Mexiterpes sabinus Causey, 1963, Psyche, 70: 235, figs. 1–3, ♂.

Types. Male holotype from Sotáno del Arroyo, 8 mi. north of Valles, San Luis Potosí, Mexico, in MCZ, examined.

Notes. I examined the type specimen in detail and found Causey's (1963b) illustrations misleading. The drawings presented here (Figs. 529–531) were made from the gonopods of the holotype, under high magnification; details were confirmed by temporarily mounting the gonopods in glycerine on a microscope slide and examining them under phase contrast. The posterior gonopods are permanently mounted on a slide and cleared almost to transparency. I found a definite gap between the posterior gonopod coxae in the midline; Causey (1963b) described them as fused. I could not find the gland opening illustrated by Causey, nor the joints between the "third and fourth" segments of the telopodite. The right posterior gonopod has a definite claw, the left does not.

Mexiterpes metallicus n. sp.
Figures 532–538

Types. Male holotype and four female paratypes from 1.2 miles east of Pinal de Amoles, Querétaro, Mexico, in an iron mine at roadside, collected 17 August 1969 by S. B. and J. Peck. The specific name is a noun in apposition: "a miner of metals."

Diagnosis. Distinct in details of the gonopods from *M. sabinus*, and in having 4 poorly pigmented ocelli.

Description of male holotype. Length, 9.7 mm. Ocelli 4, in single row (Fig. 532). Other nonsexual characters as described by Causey (1963b) for *M. sabinus*. Anterior gonopods: sternum large, well sclerotized, raised lateral lobes articulating with fused bases of coxae; coxae fused basomedially (Fig. 533), coxites elongate, gradually narrowed, sharply elbowed posteriorly, basal setae strong, numerous, setose area well defined. Coxae extending posteriorly (Fig. 537) as a lobed basal cup, firmly articulated with lateral parts of sternum. Telopodites (Figs. 534, 536) basally fused, with common basal laciniate area with deeply excavate lateral lobes; posteriorly produced into large, rugose mass. Distal part of telopodites separated, curved dorsad, sinuous. Posterior gonopods: as in Figure 535.

Description of female paratype. Nonsexual characters as described for male. Cyphopods (Fig. 538) large, protruding, similar to those of *Pseudotremia* spp.; receptacle simple, cupped, margined. Valves anteriorly fused, groove rimmed and setose; median valve of each side drawn out as heavily sclerotized hook. Sternum 3 flattened but not otherwise modified.

Notes. Though the holotype and paratype were collected in a mine, there are numerous limestone caves in the area, which should be thoroughly searched for this species. There may be epigean species of *Mexiterpes;* a female from Querétaro was tentatively assigned to *Austrotyla* (Conotylidae) when I examined it before seeing specimens of *Mexiterpes metallicus* (Shear, 1971).

LITERATURE CITED

ATTEMS, C. 1898. Neues über paläarktische Myriapoden. Zool. Jarb., Abt. Syst., **12:** 286–336.

———. 1907. Javanische Myriapoden gesammelt von Direktor K. Kraepelin im Jahre 1903. Ann. Naturhist. Mus. Wien, **24:** 78–138.

———. 1959. Die Myriapoden der Höhlen Balkanhalbinsel nach dem Material der "Biospeologica balkana." Ann. Naturh. Mus. Wien, **63:** 345–351.

BARR, T. C. 1961. Caves of Tennessee. Tennessee Dept. Conserv. Comm., Div. Geol., Bull. **64:** 1–567.

———. 1967. A new *Pseudanophthalmus* from an epigean environment in West Virginia. Psyche, **74:** 166–172.

BOLLMAN, C. H. 1888. Notes upon a collection of myriapoda from east Tennessee, with description of a new genus and six new species. Ann. New York Acad. Sci., **10:** 106–112.

———. 1893. The Myriapoda of the United States. U. S. Nat. Mus. Bull., **43:** 1–210.

BRÖLEMANN, H. W. 1918. Quelques indices

d'évolution chez les Myriapodes. Tr. Inst. Zool. Univ. Montpellier, **28:** 1–33.

———. 1922. Notes on female paraiulids. Ann. Entomol. Soc. America, **15:** 281–307.

———. 1935. Myriapodes diplopodes (Chilognathes I). *In* Faune de France, 29: 1–369.

———, AND J. L. LICHTENSTEIN. 1919. Les vulves des diplopodes (memoire preliminaire). Arch. Zool. Exper. Gen., **58:** 173–218.

BUCKETT, J. S., AND M. R. GARDNER. 1967. A new family of cavernicolous millipedes with the description of a new genus and species from Idaho (Diplopoda: Chordeumida: Chordeumidia). Michigan Entomol., **1:** 117–126.

CAUSEY, N. B. 1951a. New cleidogonid millipeds (Chordeumoidea). J. Washington Acad. Sci., **41:** 78–83.

———. 1951b. New genera and species of chordeumoid millipeds in the United States, and notes on some established species. Proc. Biol. Soc. Washington, **64:** 117–124.

———. 1952. Four new chordeumoid millipeds from the United States. Proc. Biol. Soc. Washington, **65:** 111–118.

———. 1954. Three new species and new records of southern millipeds. Tulane Stud. Zool., **2:** 63–68.

———. 1957. New records and descriptions of millipeds of the family Cleidogonidae. J. Kansas Entomol. Soc., **30:** 114–120.

———. 1958. New records and descriptions of a new genus and a new species of milliped of the family Striariidae. Proc. Biol. Soc. Washington, **71:** 179–184.

———. 1959. A new species of *Ozarkogona* from Indiana. J. Kansas Entomol. Soc., **32:** 141–144.

———. 1960a. The troglobitic milliped genus *Zygonopus*. J. New York Entomol. Soc., **68:** 69–80.

———. 1960b. *Speostriaria*, new genus. Proc. Biol. Soc. Washington, **73:** 25–28.

———. 1961. Three new millipeds of the genus *Cleidogona* (Cleidogonidae: Chordeumida) from the southern states. Florida Entomol., **44:** 35–39.

———. 1963a. Two new caseyid millipeds from California caves. Wasmann J. Biol., **21:** 193–198.

———. 1963b. *Mexiterpes sabinus*, new genus and new species, a Mexican troglobite. Psyche, **70:** 235–239.

———. 1967. *Trichopetalum subterraneum*, new species from Kentucky, new records and a key to the genus. Proc. Biol. Soc. Washington, **80:** 117–122.

CHAMBERLIN, R. V. 1910. Diplopoda from the western states. Ann. Entomol. Soc. America, **3:** 233–262.

———. 1922. The millipeds of Central America. Proc. U. S. Nat. Mus., **60:** 1–75.

———. 1925. Notes on some centipeds and millipeds from Utah. Pan-Pacific Entomol., **2:** 55–63.

———. 1940. On some chilopods and diplopods from North Carolina. Canadian Entomol., **72:** 56–59.

———. 1941a. Seven new millipeds from Mexico. Entomol. News, **52:** 250–255.

———. 1941b. New southern millipeds. Bull. Univ. Utah, **32:** 1–19.

———. 1942. On centipeds and millipeds from Mexican Caves. Bull. Univ. Utah, **33:** 1–19.

———. 1943. On Mexican millipeds. Bull. Univ. Utah, **34:** 1–103.

———. 1946. On some millipeds of Georgia. Entomol. News, **57:** 149–153.

———. 1949. A new family in the diplopod Order Chordeumida. Proc. Biol. Soc. Washington, **62:** 7–8.

———. 1952. Further records and descriptions of American millipeds. Great Basin Nat., **12:** 13–34.

———, AND R. L. HOFFMAN. 1950. On some genera and families of North American diplopods. Nat. Hist. Misc., No. 71: 1–7.

———, AND ———. 1958. Checklist of the millipeds of North America. U. S. Nat. Mus. Bull., **212:** 1–236.

———, AND S. MULAIK. 1941. On a collection of millipeds from Texas and New Mexico. J. New York Entomol. Soc., **49:** 60–64.

COOK, O. F. 1895. On recent diplopod names. Brandtia, **2:** 5–8.

———. 1899. The diplopod family Striariidae. Proc. U. S. Nat. Mus., **21:** 667–676.

———, AND G. N. COLLINS. 1895. The Craspedosomatidae of North America. Ann. New York Acad. Sci., **9:** 1–100.

COPE, E. D. 1869. Synopsis of the extinct Mammalia . . . with observations on some Myriapoda. . . . Proc. Amer. Philos. Soc., **11:** 171–192.

CORE, E. L. 1955. Cranberry Glades Natural Area. Wild Flower, **31:** 65–81.

COYLE, F. A. 1968. The mygalomorph spider genus *Atypoides* (Araneae: Antrodiaetidae). Psyche, **75:** 157–194.

DARLINGTON, P. J., JR. 1957. Zoogeography: The Geographical Distribution of Animals. New York, John Wiley & Sons. 675 pp.

———. 1965. Biogeography of the Southern End of the World. Cambridge, Harvard Univ. Press. 236 pp.

DAVIES, W. K. 1949. Caverns of West Virginia. West Virginia Geol. Surv. Report, 19: 1–353.

DEAROLF, K. 1937. The invertebrates of 75 caves in the United States. Pennsylvania Acad. Sci., **37**: 225–241.

DOUGLAS, H. H. 1964. Caves of Virginia. Falls Church, Virginia Cave Survey. 761 pp.

FRYE, J. C., H. B. WILLMAN, AND R. F. BLACK. 1965. Outline of the glacial geology of Illinois and Wisconsin. *In* H. E. Wright, Jr. and D. G. Frey (eds.), The Quaternary of the United States. Princeton, N. J., Princeton University Press, pp. 43–61.

HOFFMAN, R. L. 1950a. A preliminary list of the cleidogonid millipeds, with descriptions of a new genus from Guatemala and a new species from Virginia. J. Washington Acad. Sci., **40**: 87–92.

———. 1950b. Systematic notes on some Central American millipeds. Proc. Biol. Soc. Washington, **63**: 69–72.

———. 1950c. Records and descriptions of diplopods from the southern Appalachians. J. Elisha Mitchell Sci. Soc., **66**: 11–33.

———. 1958. On the identity of *Pseudotremia cavernarum* Cope, a poorly known American chordeumoid diplopod. Proc. Biol. Soc. Washington, **71**: 113–118.

———. 1961. Systematic and morphological notes on North American conotyloid diplopods. Trans. Amer. Entomol. Soc., **87**: 259–272.

———. 1962. A new genus and species in the diplopod family Nearctodesmidae from Illinois (Polydesmida). American Midl. Nat., **68**: 192–198.

———. 1963. Notes on the structure and classification of the diplopod family Heterochordeumatidae. Ann. Mag. Nat. Hist., **6**: 129–135.

———. 1969a. The origin and affinities of the southern Appalachian diplopod fauna. *In* P. C. Holt (ed.), The distributional history of the biota of the southern Appalachians, Part I, Invertebrates. Virginia Polytech. Inst. Res. Monogr., 1. 295 pp.

———. 1969b. Myriapoda, exclusive of Insecta, pp. R572–R606. *In* R. C. Moore (ed.), Treatise on Invertebrate Paleontology, Part R, Arthr. 4, Vol. 2. Lawrence, Kansas, Geological Society of America. Pp. R400–R659.

———, AND R. E. CRABILL. 1953. C. S. Rafinesque as the real father of American myriapodology: an analysis of his hitherto unrecognized species. Florida Entomol., **36**: 73–82.

JEEKEL, C. A. 1969. Two new generic names in the diplopod order Craspedosomatida. Entomol. Bericht., **29**: 88.

KAESTNER, A. 1968. Invertebrate Zoology, vol. 2, translated and adapted by H. W. and L. R. Levi. New York, Wiley-Interscience. 472 pp.

KEETON, W. T. 1960. A taxonomic study of the milliped family Spirobolidae. Mem. American Entomol. Soc., **17**: 1–146.

KRAUS, O. 1954. Myriapoden aus El Salvador. Senck. Biol., **35**: 293–349.

LOOMIS, H. F. 1939. The millipeds collected in Appalachian Caves by Mr. Kenneth Dearolf. Bull. Mus. Comp. Zool., **86**: 165–193.

———. 1943. New cave and epigean millipeds. Bull. Mus. Comp. Zool., **92**: 373–410.

———. 1944. Millipeds principally collected by Professor V. E. Shelford in the eastern and southeastern states. Psyche, **51**: 166–177.

———. 1959. Millipeds collected en route from Florida to San Antonio, Texas. J. Washington Acad. Sci., **49**: 157–163.

———. 1963. Millipeds from states immediately north and south of the Mexican boundary. J. Kansas Entomol. Soc., **36**: 118–126.

———. 1964. The millipeds of Panama (Diplopoda). Fieldiana (Zool.), **47**: 5–136.

———. 1966. Two new families and other North American Diplopoda of the order Chordeumida. Proc. Biol. Soc. Washington, **79**: 221–230.

———. 1968. A checklist of the millipeds of Mexico and Central America. U. S. Nat. Mus. Bull., **266**: 1–137.

MCNEILL, J. 1887. Descriptions of twelve new species of Myriapoda, chiefly from Indiana. Proc. U. S. Nat. Mus., **10**: 328–334.

MALDONADO-KOERDELL, M. 1964. Geohistory and paleogeography of middle America. *In* R. C. West (ed.), Handbook of Middle American Indians, Vol. I. Austin, Univ. of Texas Press. 570 pp.

MANTON, S. M. 1953. The evolution of arthropodan locomotory mechanisms — Part 4. The structure, habits and evolution of the Diplopoda. J. Linnean Soc., **42**: 299–368.

MITCHELL, R. W. 1968. *Typhlochactas,* a new genus of eyeless cave scorpion from Mexico. Ann. Speleol., **23**: 753–777.

———. 1969. A comparison of temperate and tropical cave communities. Southwestern Nat. **14**: 73–88.

MURAKAMI, Y., AND K. Y. PAIK. 1968. Results of the speological survey in South Korea, 1966. XI. Cave-dwelling myriapods from the southern part of Korea. Bull. Nat. Sci. Mus. (Tokyo), **11**: 363–384.

PACKARD, A. S. 1883. A revision of the Lysiopetalidae, a family of Chilognath Myriapoda, with a notice of the genus *Cambala*. Proc. Amer. Philos. Soc., **21**: 177–197.

Palisot de Beauvois, A. M. 1805. Insectes . . . Aptères: 1–276 (original not seen, as reported in Hoffman and Crabill, 1953).

Palmén, E. 1952. Survey of the Diplopoda of Newfoundland. Ann. Zool. Soc. 'Vanamo,' **15**: 1–31.

Rafinesque, C. S. 1820. Annals of Nature. . . . First Annual Number for 1820. 20 pp. (original not seen, as reported in Hoffman and Crabill, 1953).

Say, T. 1821. Description of the Myriapodae of the United States. J. Acad. Nat. Sci. Philadelphia, **2**: 102–114.

Schubart, O. 1934. Tausendfüssler oder Myriapoda, I: Diplopoda. *In* F. Dahl (ed.), Die Tierwelt Deutschlands. Vol. 28. 318 pp.

Schuchert, C. 1955. Atlas of Palaeogeographic Maps of North America. New York, John Wiley and Sons. 177 pp.

Silvestri, F. 1903. Note diplopodologiche. I. Nuovi diplopodi del Chile. Boll. Mus. Torino, **18**: 1–12.

———. 1913. Illustrazione di due famiglie di Chordeumoidea (Diplopoda) del Nord America. Boll. Lab. Zool. (Portici), **7**: 303–310.

Shear, W. A. 1969. A synopsis of the cave millipeds of the United States, with an illustrated key to genera. Psyche, **76**: 126–143.

———. 1971a. A taxonomic revision of the milliped family Conotylidae in North America, with a description of the new family Adritylidae (Diplopoda: Chordeumida). Bull. Mus. Comp. Zool., **141**(2): 55–96.

———. 1971b. The taxonomic position of the milliped *Ergethus perditus* (Polydesmida, Paradoxosomatidae). Proc. Biol. Soc. Washington, **83**(39): 455–458.

———, and H. W. Levi. 1970. Cleaning museum specimens of Arachnida and Myriapoda with ultrasonics. Bull. Brit. Arachn. Soc., **1**: 1–117.

Strasser, K. 1942. Diplopoden aus dem Julischen Karst. Zool. Anz., **138**: 15–234.

Underwood, L. M. 1893. A review of the literature of the North American Myriapoda. *In* C. H. Bollman, the Myriapoda of North America. U. S. Nat. Mus. Bull., **46**: 9–18.

Verhoeff, K. W. 1906. Uber Diplopoden 5. (24) Aufsatz. Arch. Naturg., **72**: 107–226.

———. 1909. Neues System der Diplopoden — Ascospermophora. Zool. Anz., **34**: 566–572.

———. 1910. Über Diplopoden. 11–15 Aufsatz (31–35). Nov. Act. Abh. Kaiserl. Leop.-Carol. Deutsch. Akad. Naturforsch., **92**: 144–146.

———. 1913. Zwei neue Gattungen der Trachyzona superfam. der Ascospermophora. Zool. Anz., **43**: 125–143.

———. 1914. Ascospermorphoren aus Japan. (Über Diplopoden 69. Aufsatz.). Zool. Anz., **43**: 342–370.

———. 1932. Diplopoden-Beiträge. Zool. Jahrb., Abt. Syst., **62**: 459–524.

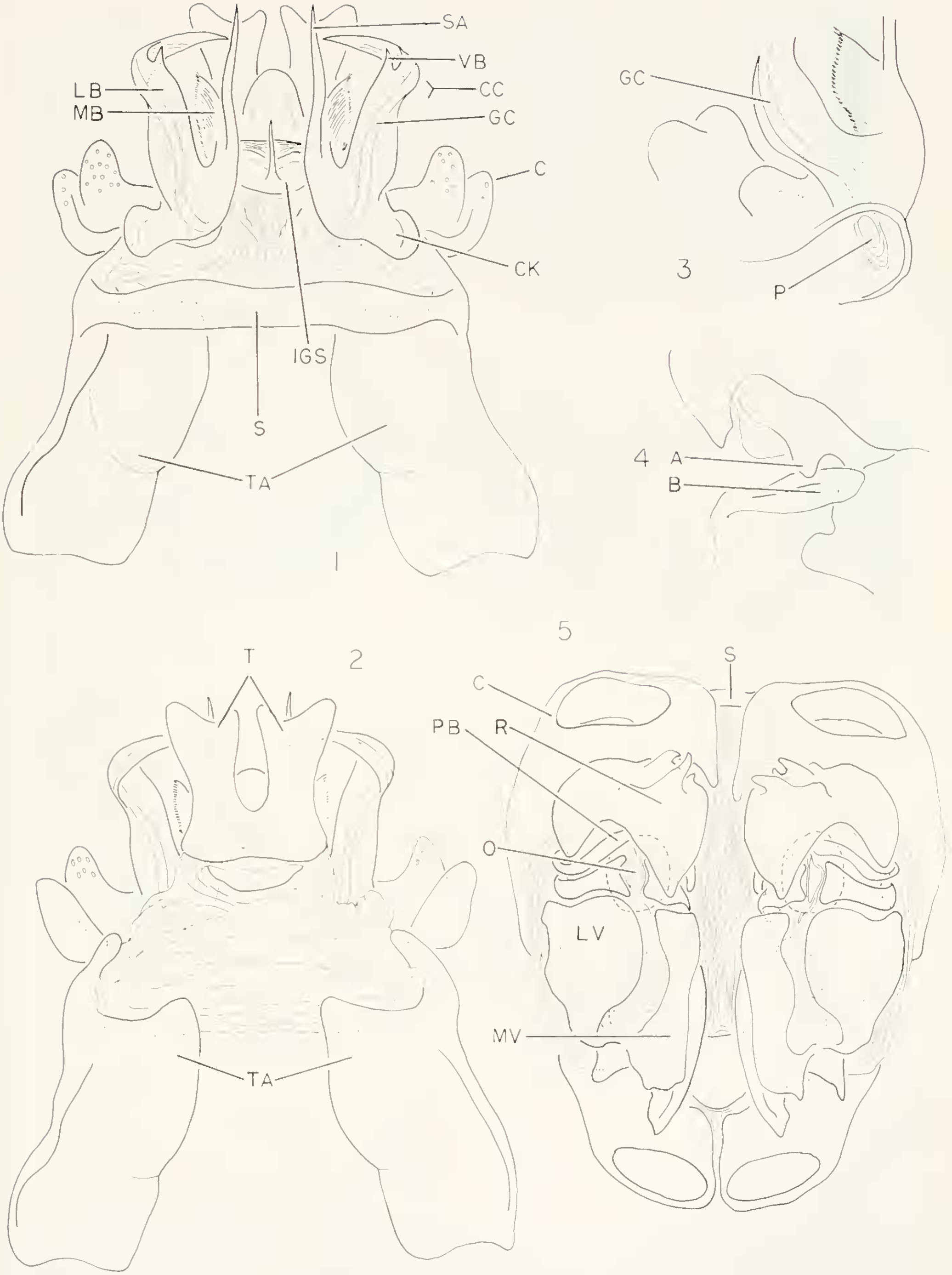
———. 1935. Neues ostasiatische Diplopoden. Zool. Anz., **107**: 62–73.

———. 1936. Ueber Diplopoden aus Japan, gesammelt von Herrn Y. Takakuwa (139. Diplopoden-Aufsatz). Trans. Sapporo Nat. Hist. Soc., **14**: 148–171.

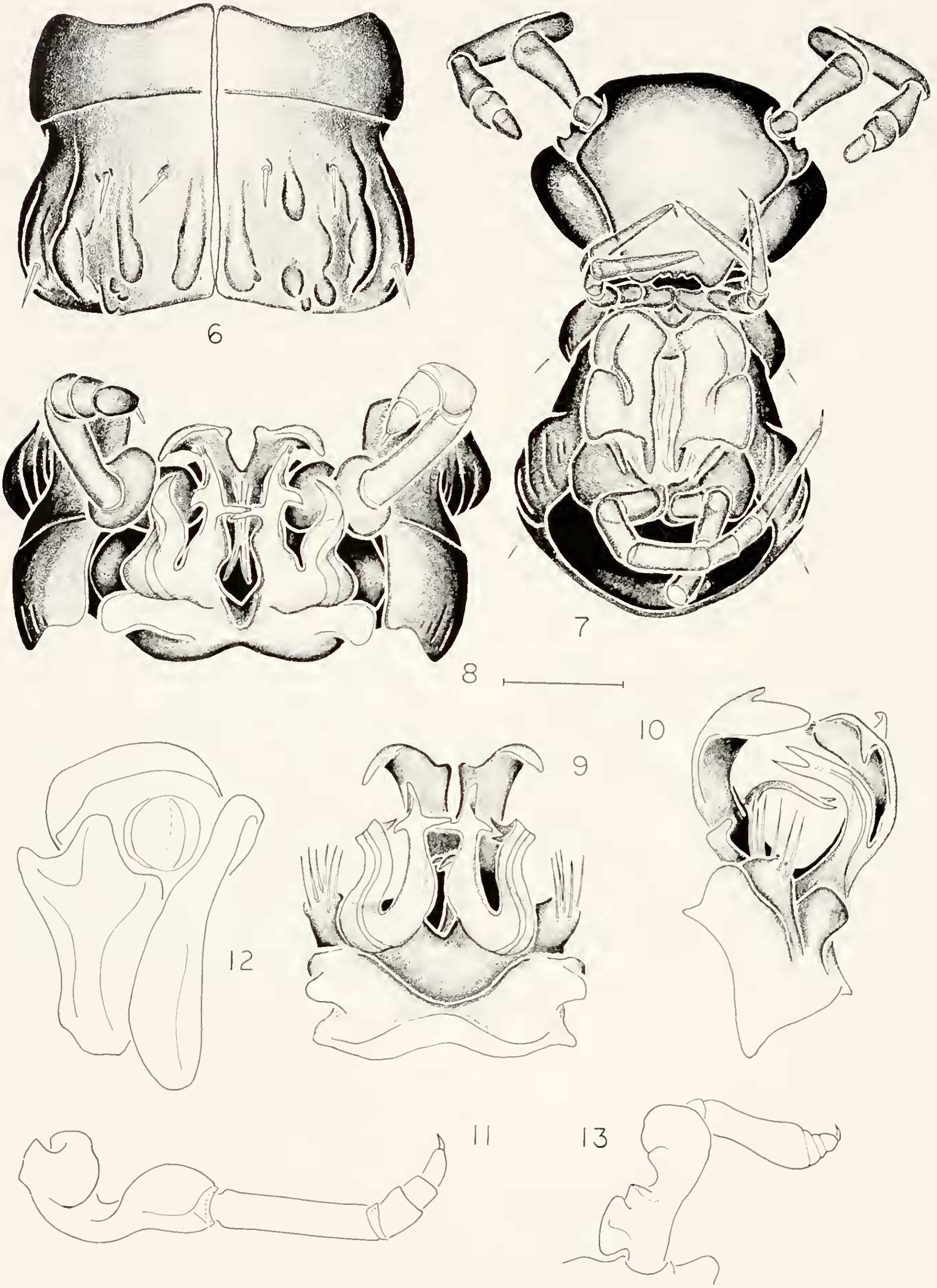
Westcott, R. 1968. A new subfamily of blind beetles from Idaho ice caves. . . . Contr. Sci. Los Angeles County Mus. Nat. Hist., **141**: 1–14.

Williams, S. R., and R. A. Hefner. 1928. Millipedes and centipedes of Ohio. Ohio Biol. Surv. Bull., **28**: 93–146.

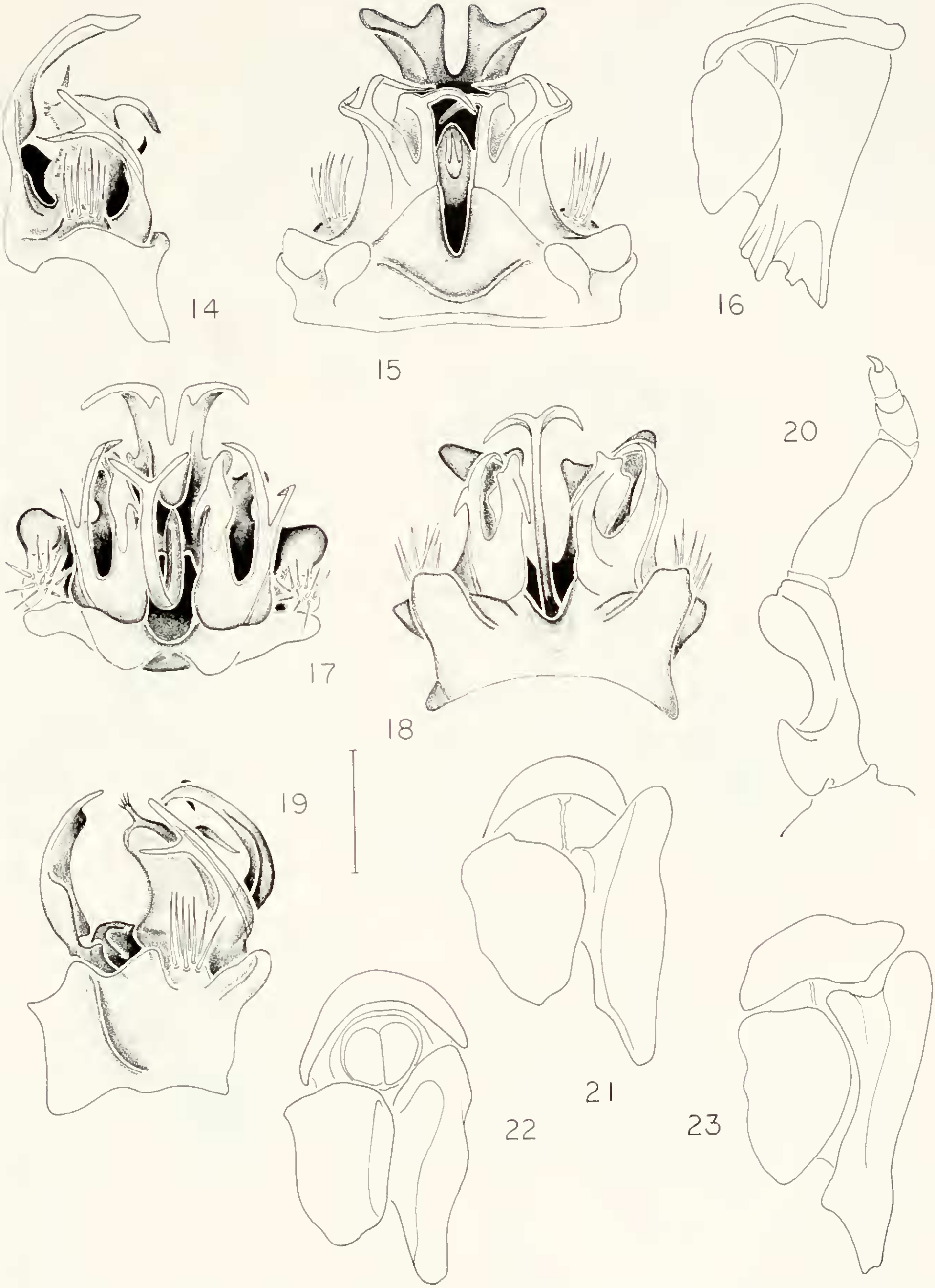
Wood, H. C. 1865. The Myriapoda of North America. Trans. American Philos. Soc., **13**: 137–248.



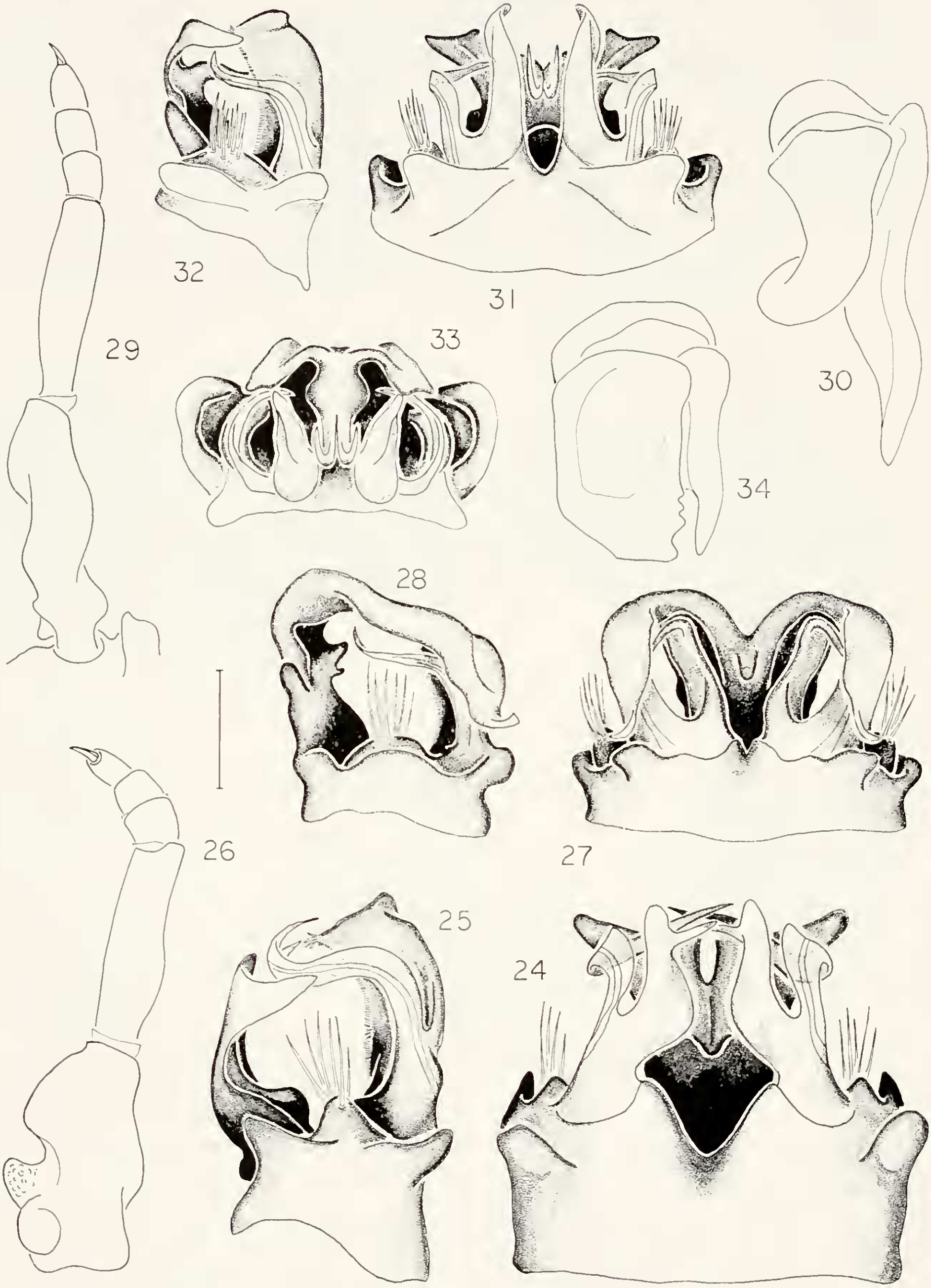
Figures 1–5. Anatomy of genitalia of *Pseudatremia hobbsi*. Fig. 1. Gonopods, anterior view. Fig. 2. Gonopods, posterior view. Fig. 3. Base of gonopod coxa, subdorsal view. Fig. 4. Articulation of gonopod sternum and coxa, lateral view. Fig. 5. Cyphopods and associated leg coxae, ventral view.



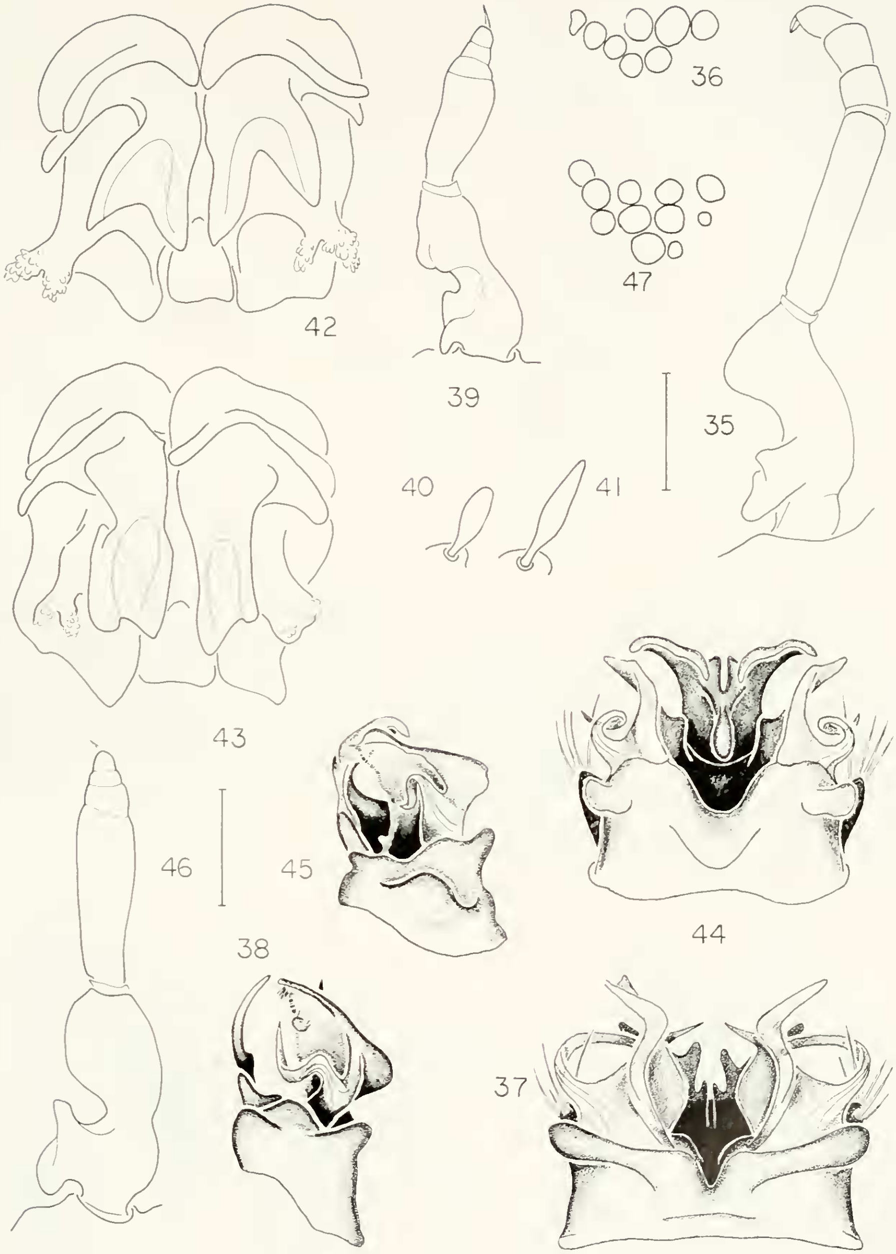
Figures 6–13. Anatomy of *Pseudotremia* species. Fig. 6. Tenth segment of *P. nyx*, dorsal view. Fig. 7. Anterior end of female *P. lethe*, ventral view. Fig. 8. Seventh segment of male *P. nefanda*, ventral view. Figs. 9–12. *P. nefanda*. Fig. 9. Gonopods, anterior view. Fig. 10. Left gonopod, lateral view. Fig. 11. Right posterior gonopod, anterior view. Fig. 12. Right cyphopod, ventral view. Fig. 13. Right posterior gonopod of *P. amphiorax*, anterior view. Scale lines = 0.5 mm for Figs. 6–11, 13; 0.25 mm for Fig. 12.



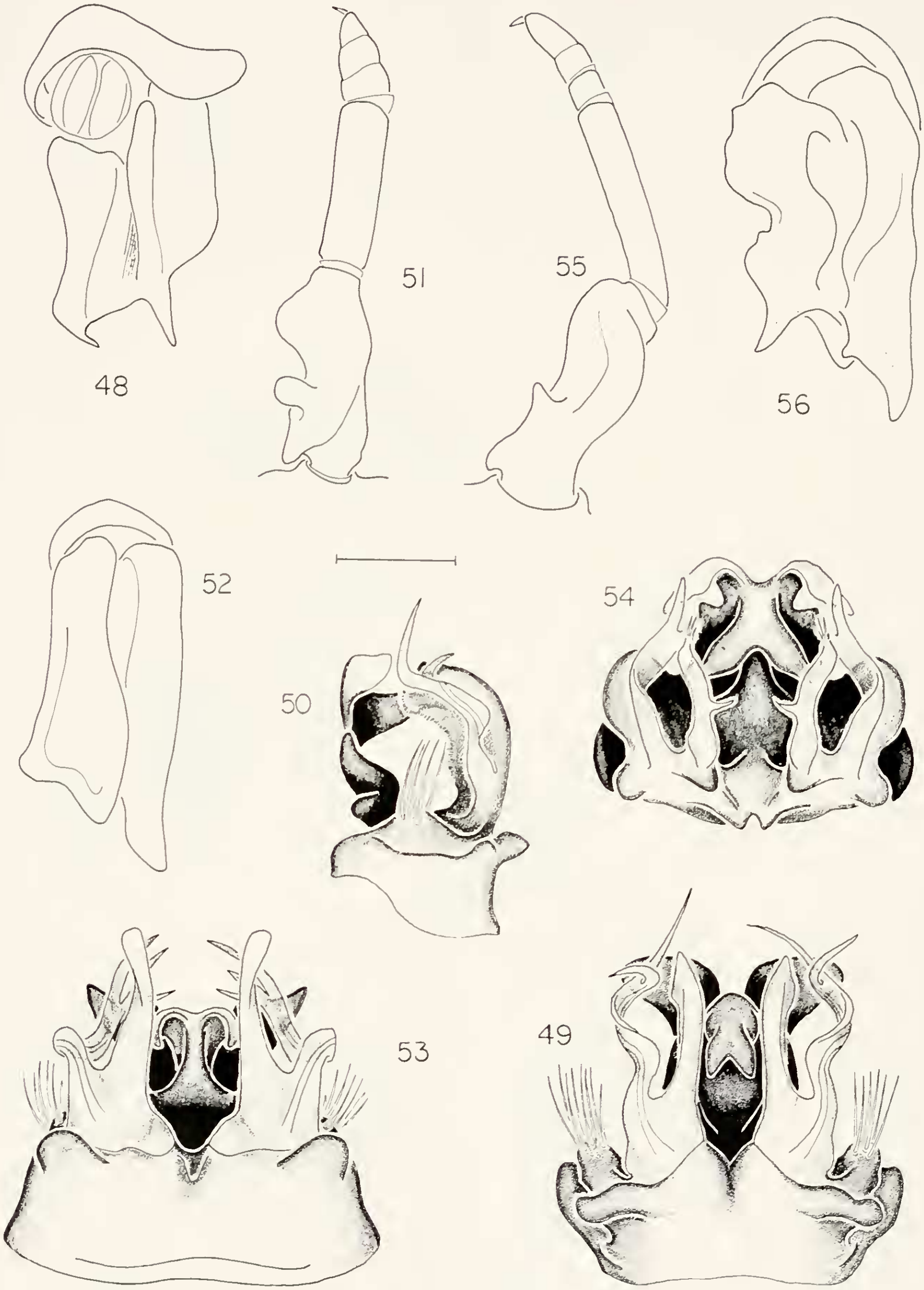
Figures 14–23. Anatomy of *Pseudotremia* spp. Figs. 14–16. *P. amphiarax*. Fig. 14. Left gonopods, lateral view. Fig. 15. Gonopods, anterior view. Fig. 16. Right cyphopod, ventral view. Figs. 17–23. *P. indianae*. Fig. 17. Gonopods, ventral view. Fig. 18. Gonopods, anterior view. Fig. 19. Left gonopod, lateral view. Fig. 20. Right posterior gonopod, anterior view. Figs. 21–23. Right cyphopods, ventral view. Fig. 21. Specimen from King's Cave. Fig. 22. Specimen from Mayfield's Cave. Fig. 23. Specimen from Wyandotte Cave. Scale lines = 0.5 mm for anterior and posterior gonopods, 0.25 mm for cyphopods.



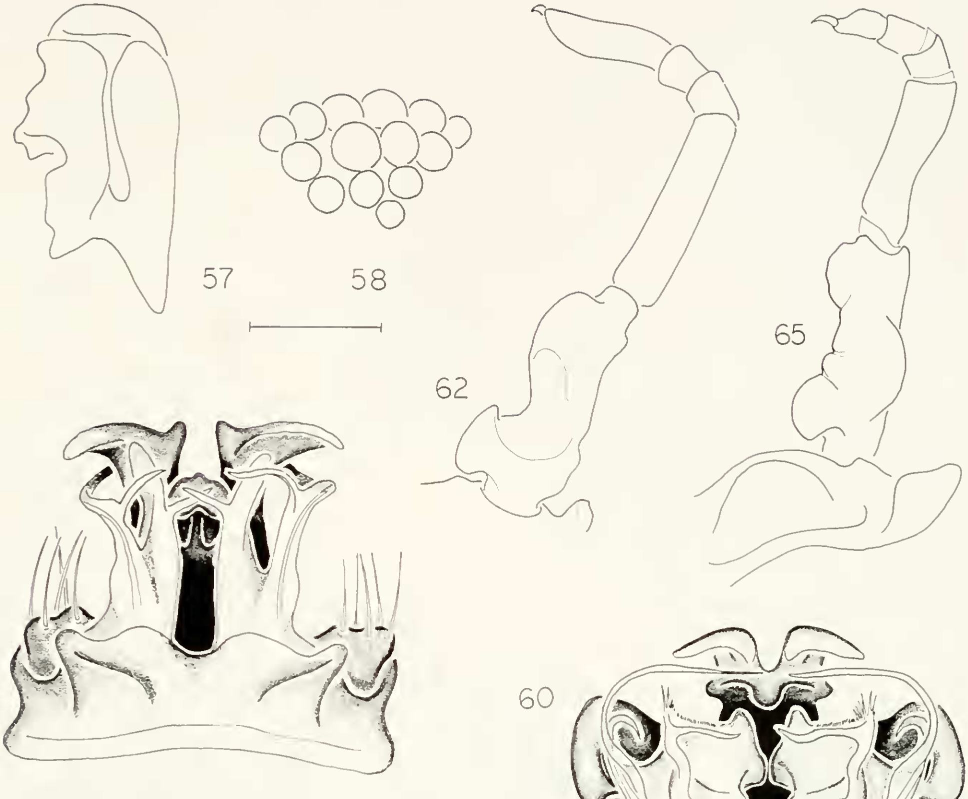
Figures 24–34. Anatomy of *Pseudotremia* spp. Figs. 24–26. *P. valga*. Fig. 24. Anterior gonopods, anterior view. Fig. 25. Left anterior gonopods, lateral view. Fig. 26. Right posterior gonopod, anterior view. Figs. 27–30. *P. stupefactor*. Fig. 27. Anterior gonopods, anterior view. Fig. 28. Left anterior gonopod, lateral view. Fig. 29. Right posterior gonopod, anterior view. Fig. 30. Right cyphopod, ventral view. Figs. 31–34. *P. merops*. Fig. 31. Anterior gonopods, anterior view. Fig. 32. Left anterior gonopod, lateral view. Fig. 33. Anterior gonopods, ventral view. Fig. 34. Right cyphopod, ventral view. Scale lines = 0.5 mm for anterior and posterior gonopods, 0.25 mm for cyphopods.



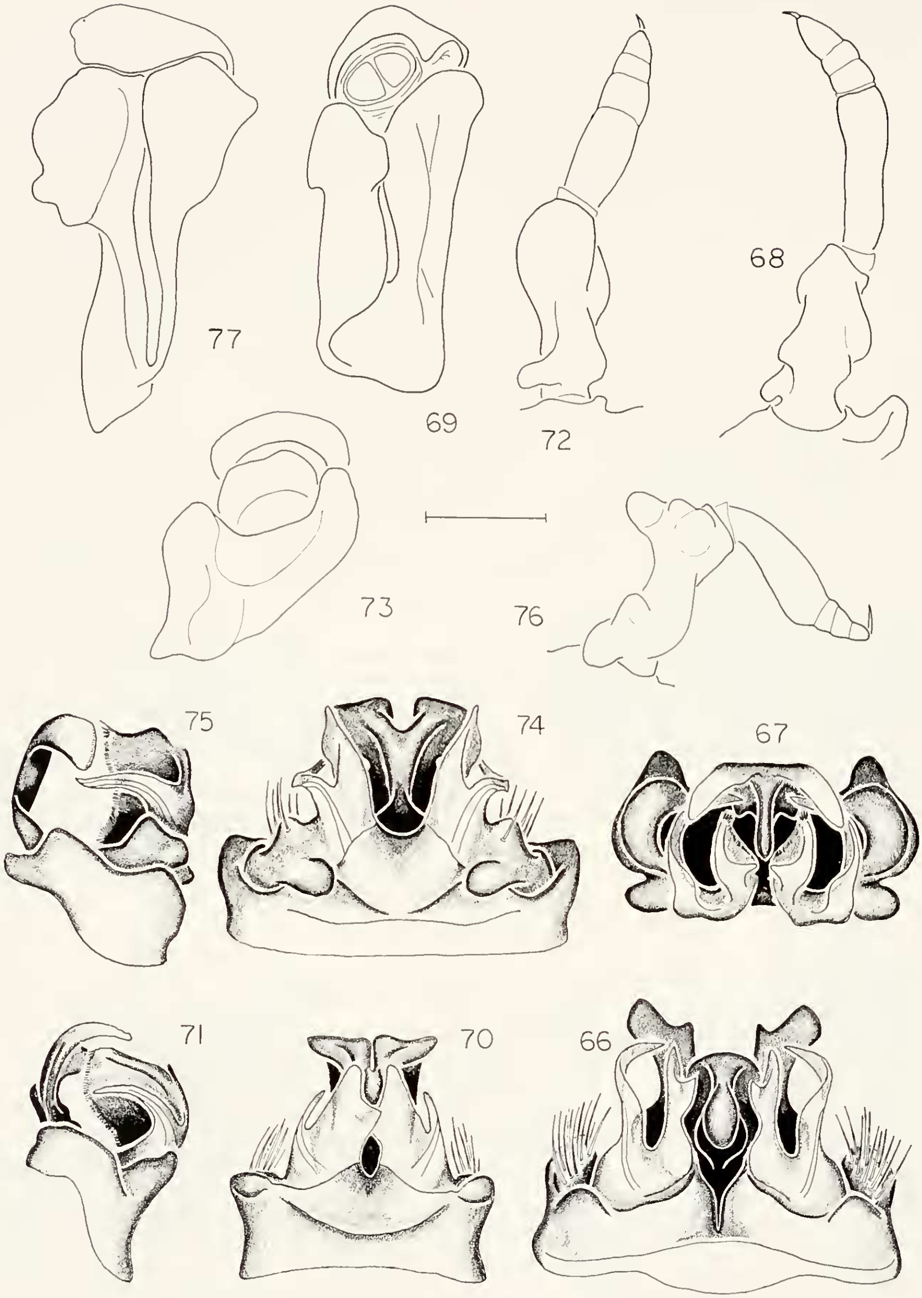
Figures 35–47. Anatomy of *Pseudotremia* spp. Fig. 35. Right posterior gonopod of *P. merops*, anterior view. Figs. 36–43. *P. unca*. Fig. 36. Left eyepatch, lateral view. Fig. 37. Anterior gonopods, anterior view. Fig. 38. Left anterior gonopod, setae omitted, lateral view. Fig. 39. Right posterior gonopod, anterior view. Fig. 40. Outer segmental seta from segment five. Fig. 41. Outer segmental seta from segment 21. Fig. 42. Cyphopods, ventral view. Fig. 43. Cyphopods of another specimen from the same locality, ventral view. Figs. 44–47. *P. spira*. Fig. 44. Anterior gonopods, anterior view. Fig. 45. Left anterior gonopod, setae omitted, lateral view. Fig. 46. Right posterior gonopod, anterior view. Fig. 47. Left eyepatch, lateral view. Scale lines = 0.5 mm for anterior and posterior gonopods, 0.25 mm for cyphopods.



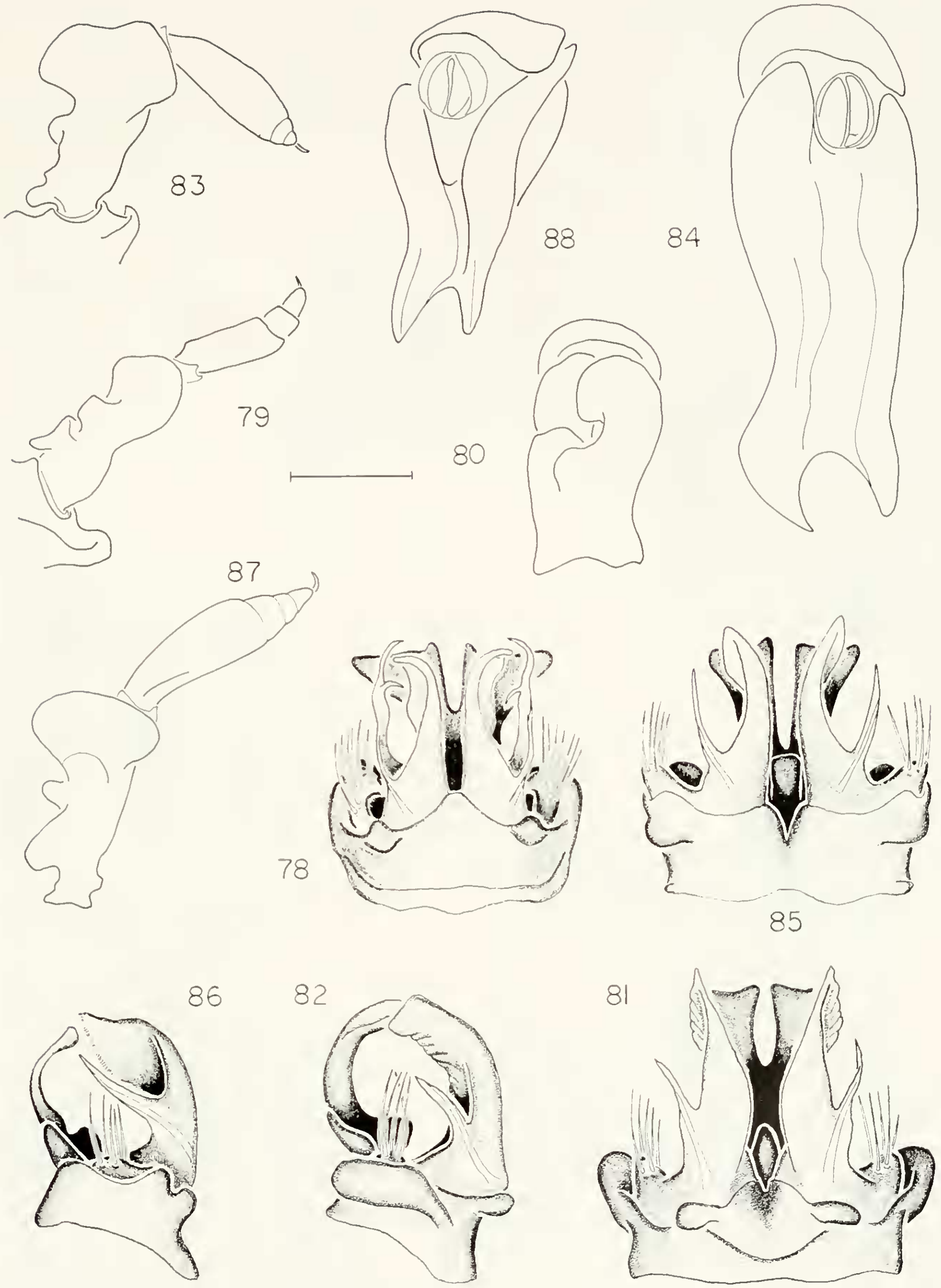
Figures 48–56. Anatomy of *Pseudotremia* spp. Fig. 48. Right cyphopod of *P. spira*, ventral view. Figs. 49–52. *P. acheron*. Fig. 49. Anterior gonopods, anterior view. Fig. 50. Left anterior gonopod, lateral view. Fig. 51. Right posterior gonopod, anterior view. Fig. 52. Right cyphopod, ventral view. Figs. 53–56. *P. rhadamanthus*. Fig. 53. Anterior gonopods, anterior view. Fig. 54. Anterior gonopods, ventral view. Fig. 55. Right posterior gonopod, anterior view. Fig. 56. Right cyphopod of specimen from Terrill's Cave, ventral view. Scale lines = 0.5 mm for anterior and posterior gonopods, 0.25 mm for cyphopods.



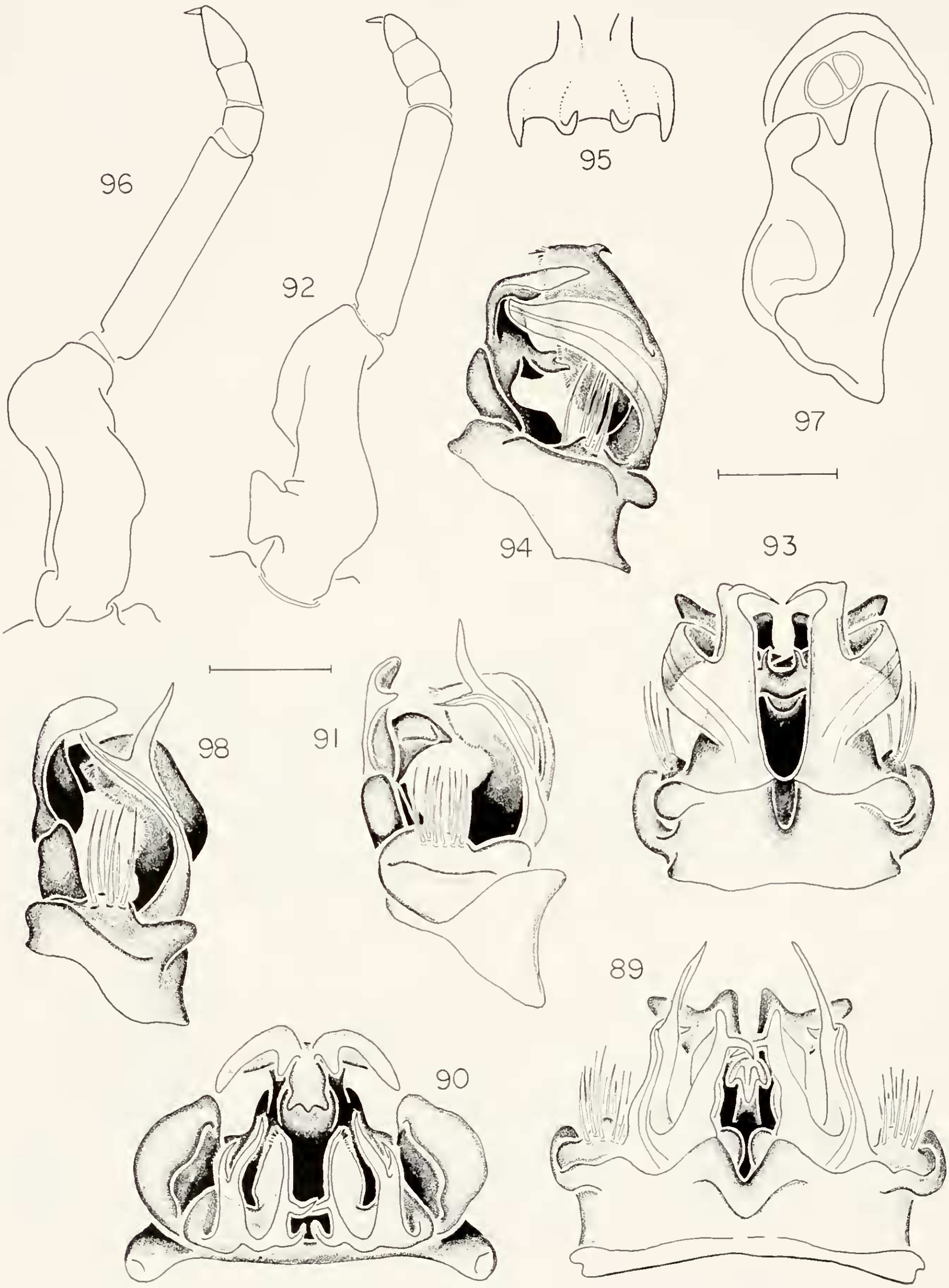
Figures 57–65. Anatomy of *Pseudotremia* spp. Fig. 57. Right cyphopod of *P. rhadamanthus* from Monteagle Saltpetre Cave, ventral view. Figs. 58–62. *P. saco*. Fig. 58. Right eyepatch, lateral view. Fig. 59. Anterior gonopods, anterior view. Fig. 60. Anterior gonopods, ventral view. Fig. 61. Left anterior gonopod, lateral view. Fig. 62. Right posterior gonopod, anterior view. Figs. 63–65. *P. eburnea*. Fig. 63. Anterior gonopods, anterior view. Fig. 64. Left anterior gonopod, lateral view. Fig. 65. Right posterior gonopod and part of sternum, anterior view. Scale lines = 0.5 mm for anterior and posterior gonopods, 0.25 mm for cyphopods.



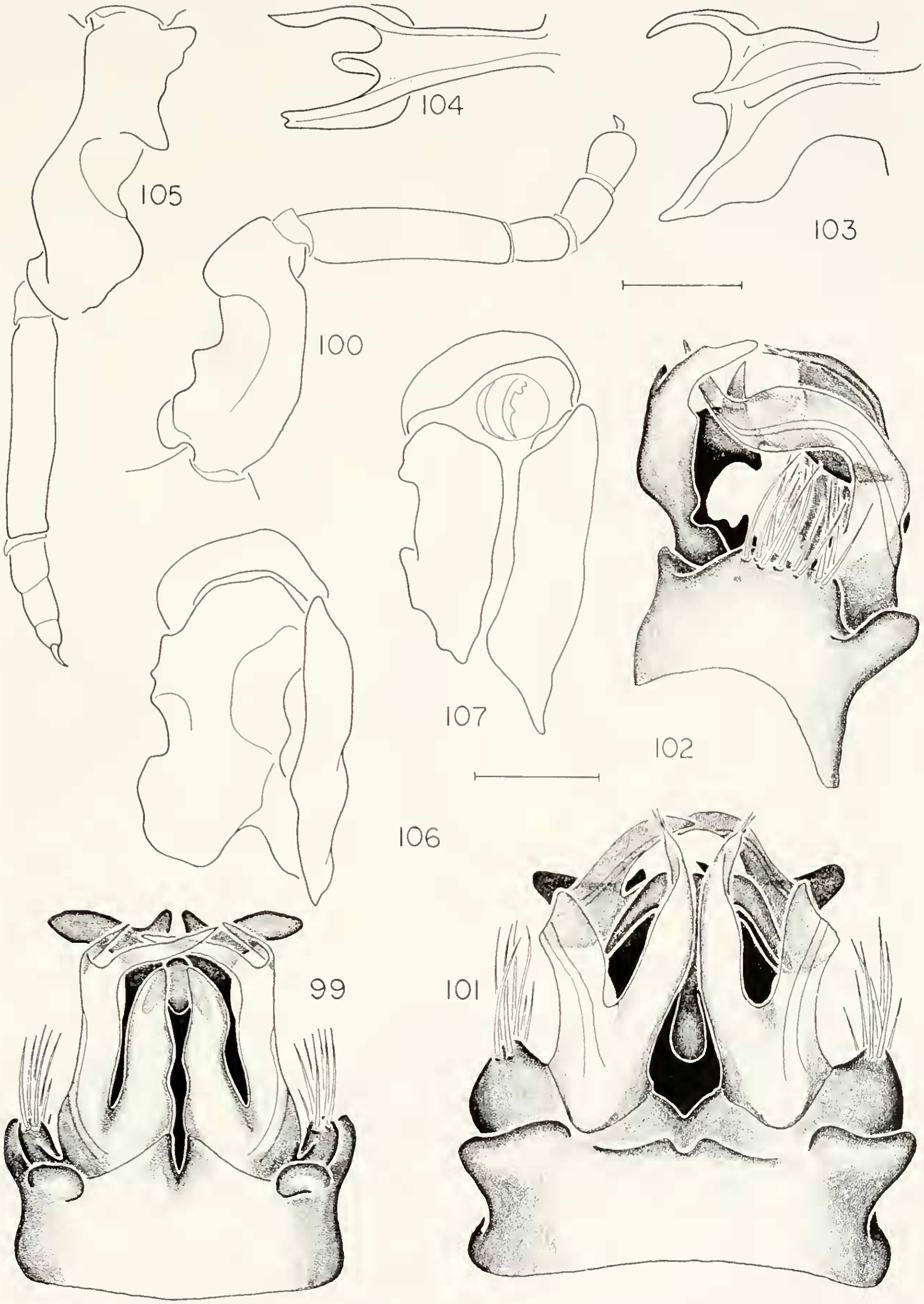
Figures 66–77. Anatomy of *Pseudotremia* spp. Figs. 66–69. *P. aeacus*. Fig. 66. Anterior gonopods, anterior view. Fig. 67. Anterior gonopods, ventral view. Fig. 68. Right posterior gonopod, anterior view. Fig. 69. Right cyphopod, ventral view. Figs. 70–73. *P. nodosa*. Fig. 70. Anterior gonopods, anterior view. Fig. 71. Left anterior gonopod, setae omitted, lateral view. Fig. 72. Right posterior gonopod, anterior view. Fig. 73. Right cyphopod, ventral view. Figs. 74–77. *P. nyx*. Fig. 74. Anterior gonopods, anterior view. Fig. 75. Left anterior gonopod, setae omitted, lateral view. Fig. 76. Right posterior gonopod, anterior view. Fig. 77. Right cyphopod, ventral view. Scale lines = 0.5 mm for anterior and posterior gonopods, 0.25 mm for cyphopods.



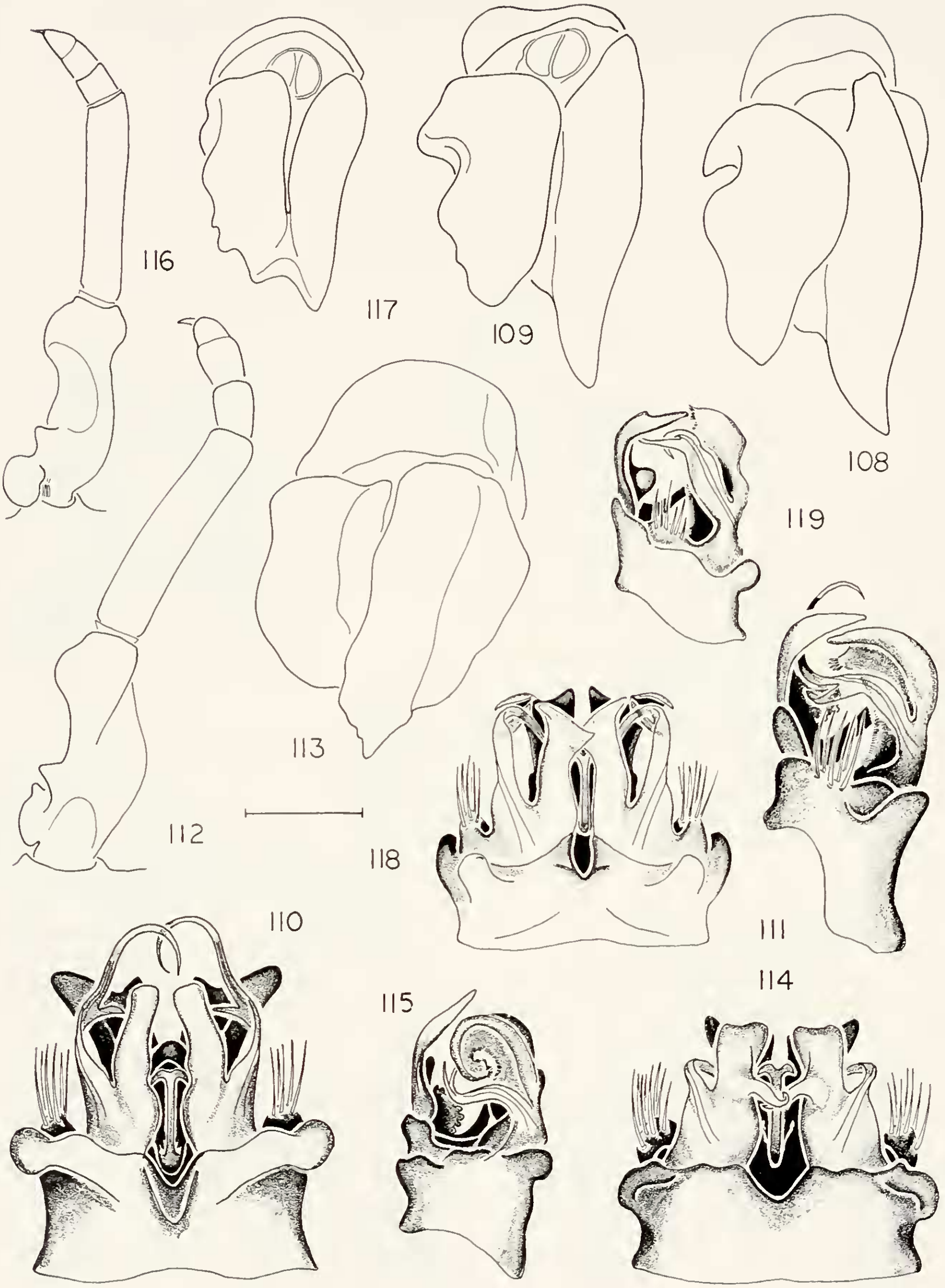
Figures 78–88. Anatomy of *Pseudotremia* spp. Figs. 78–80. *P. lethe*. Fig. 78. Anterior gonopods, anterior view. Fig. 79. Right posterior gonopod, anterior view. Fig. 80. Right cyphopod, ventral view. Figs. 81–84. *P. cercops*. Fig. 81. Anterior gonopods, anterior view. Fig. 82. Left anterior gonopod, lateral view. Fig. 83. Right posterior gonopod, anterior view. Fig. 84. Right cyphopod, ventral view. Figs. 85–88. *P. lictor*. Fig. 85. Anterior gonopods, anterior view. Fig. 86. Left anterior gonopod, lateral view. Fig. 87. Right posterior gonopod, anterior view. Fig. 88. Right cyphopod, ventral view. Scale lines = 0.5 mm for anterior and posterior gonopods, 0.25 mm for cyphopods.



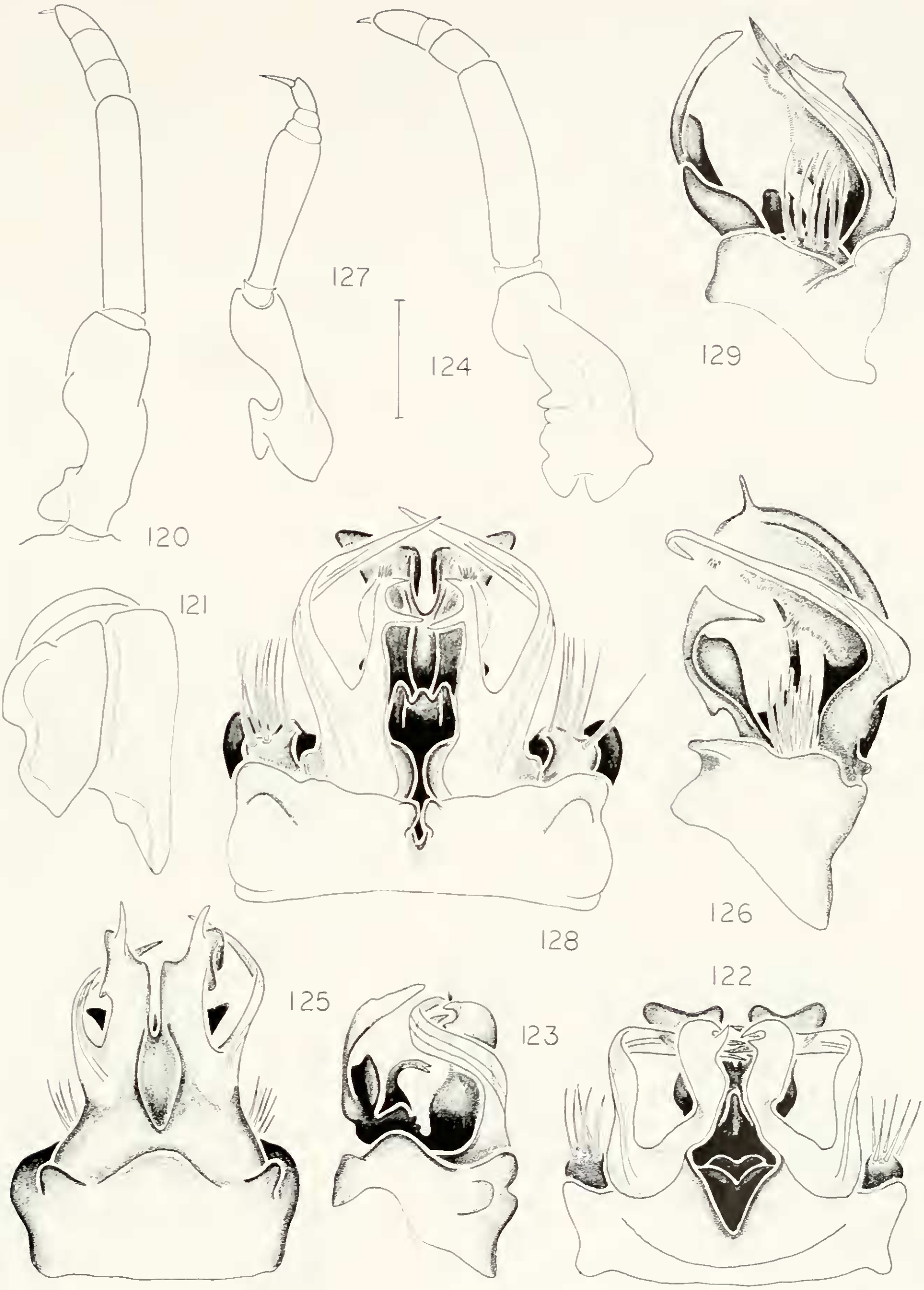
Figures 89–98. Anatomy of *Pseudatremia* spp. Figs. 89–92. *P. scrutorum*. Fig. 89. Anterior gonopods, anterior view. Fig. 90. Anterior gonopods, ventral view. Fig. 91. Left anterior gonopod, lateral view. Fig. 92. Right posterior gonopod, anterior view. Figs. 93–97. *P. minos*. Fig. 93. Anterior gonopods, anterior view. Fig. 94. Left anterior gonopod, lateral view. Fig. 95. Telopodite process of gonopods, ventral view. Fig. 96. Right posterior gonopod, anterior view. Fig. 97. Right cyphopod, ventral view. Fig. 98. Left anterior gonopod of *P. cocytus*, lateral view. Scale lines = 0.5 mm for anterior and posterior gonopods, 0.25 mm for cyphopods.



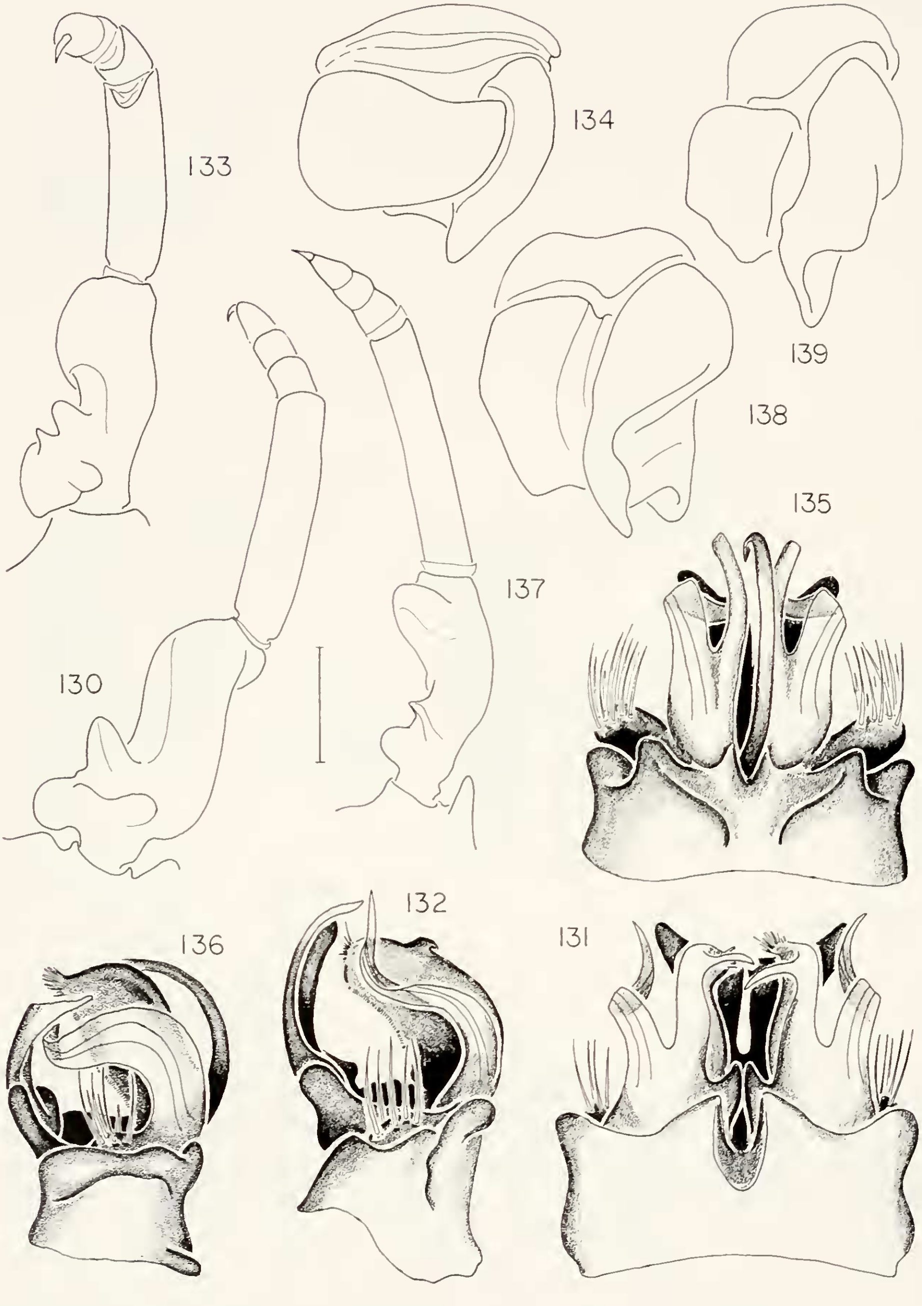
Figures 99–107. Anatomy of *Pseudotremia* spp. Figs. 99–100. *P. cocytus*. Fig. 99. Anterior gonopods, anterior view. Fig. 100. Right posterior gonopod, anterior view. Figs. 101–107. *P. cottus*. Fig. 101. Anterior gonopods, anterior view. Fig. 102. Left anterior gonopod, lateral view. Figs. 103–104. Telopodite processes of gonopods, ventrolateral views. Fig. 103. Specimen from Cade's Cove. Fig. 104. Specimen from Carden Cove. Fig. 105. Right posterior gonopod, anterior view. Figs. 106–107. Right cyphopods, ventral views. Fig. 106. Specimen from Cade's Cove. Fig. 107. Specimen from Walker's Cove. Scale lines = 0.5 mm for anterior and posterior gonopods, 0.25 mm for cyphopods.



Figures 108–119. Anatomy of *Pseudotremia* spp. Figs. 108–109. *P. cottus*, right cyphopods, ventral views. Fig. 108. Specimen from Corden's Cave. Fig. 109. Specimen from Quarry Cave #1. Figs. 110–113. *P. tuberculata*. Fig. 110. Anterior gonopods, anterior view. Fig. 111. Left anterior gonopod, lateral view. Fig. 112. Right posterior gonopod, anterior view. Fig. 113. Right cyphopod, ventral view. Figs. 114–117. *P. momus*. Fig. 114. Anterior gonopods, anterior view. Fig. 115. Left anterior gonopod, setae omitted, lateral view. Fig. 116. Right posterior gonopod, anterior view. Fig. 117. Right cyphopod, ventral view. Figs. 118–119. *P. armesi*. Fig. 118. Anterior gonopod, anterior view. Fig. 119. Left anterior gonopod, lateral view. Scale lines = 0.5 mm for anterior and posterior gonopods, 0.25 mm for cyphopods.

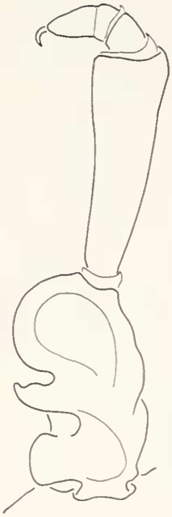


Figures 120–129. Anatomy of *Pseudotremia* spp. Figs. 120–121. *P. ormesi*. Fig. 120. Right posterior gonopod, anterior view. Fig. 121. Right cyphopod, ventral view. Figs. 122–124. *P. alecto*. Fig. 122. Anterior gonopods, anterior view. Fig. 123. Left anterior gonopod, setae omitted, lateral view. Fig. 124. Right posterior gonopod, anterior view. Figs. 125–127. *P. luscioso*. Fig. 125. Anterior gonopods, anterior view. Fig. 126. Left anterior gonopod, lateral view. Fig. 127. Right posterior gonopod, anterior view. Figs. 128–129. *P. simulans*, specimen from marsh near Franklin, W. Va. Fig. 128. Anterior gonopods, anterior view. Fig. 129. Left anterior gonopod, lateral view. Scale lines = 0.5 mm for anterior and posterior gonopods, 0.25 mm for cyphopods.



Figures 130–139. Anatomy of *Pseudotremia* spp. Fig. 130. Right posterior gonopod of *P. simulans* from marsh near Franklin, W. Va., anterior view. Figs. 131–134. *P. simulans*, holotype. Fig. 131. Anterior gonopods, anterior view. Fig. 132. Left anterior gonopod, lateral view. Fig. 133. Right posterior gonopod, anterior view. Fig. 134. Right cyphopod, paratype, ventral view. Figs. 135–139. *P. fulgida*. Fig. 135. Anterior gonopods, anterior view. Fig. 136. Left anterior gonopod, lateral view. Fig. 137. Right posterior gonopod, anterior view. Fig. 138. Right cyphopod, ventral view. Fig. 139. Right cyphopod of another specimen from the same locality, ventral view. Scale lines = 0.5 mm for anterior and posterior gonopods, 0.25 mm for cyphopods.

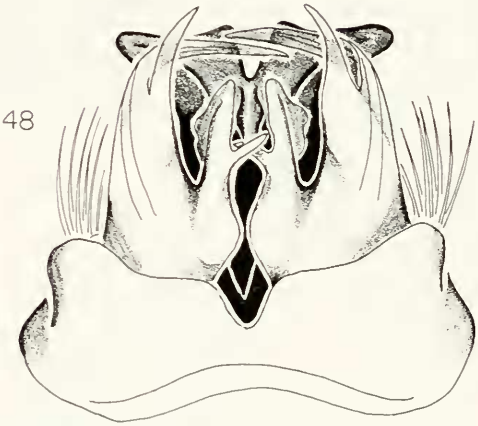
143



147

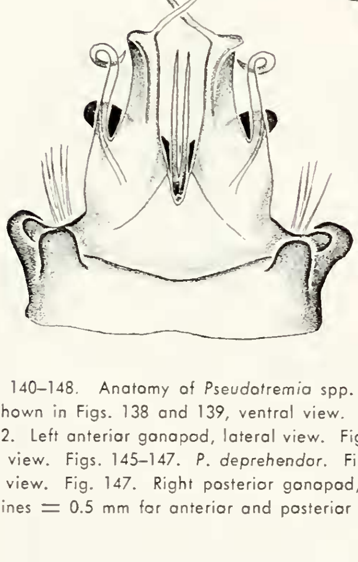
144

140



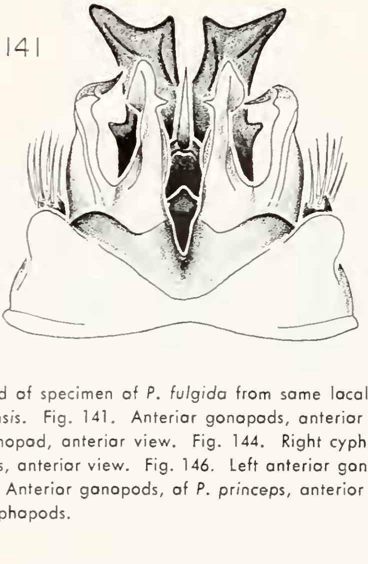
148

146



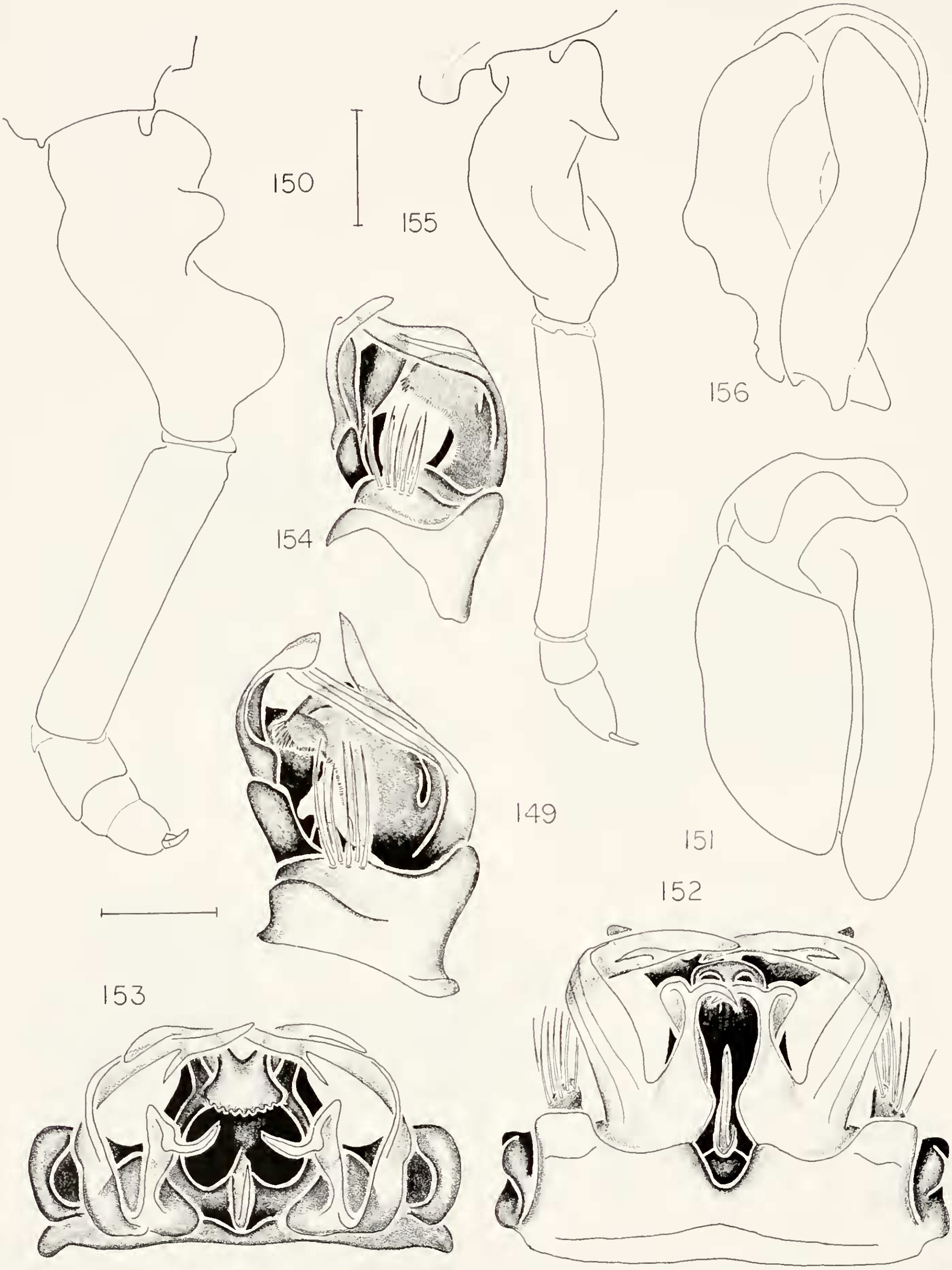
145

142

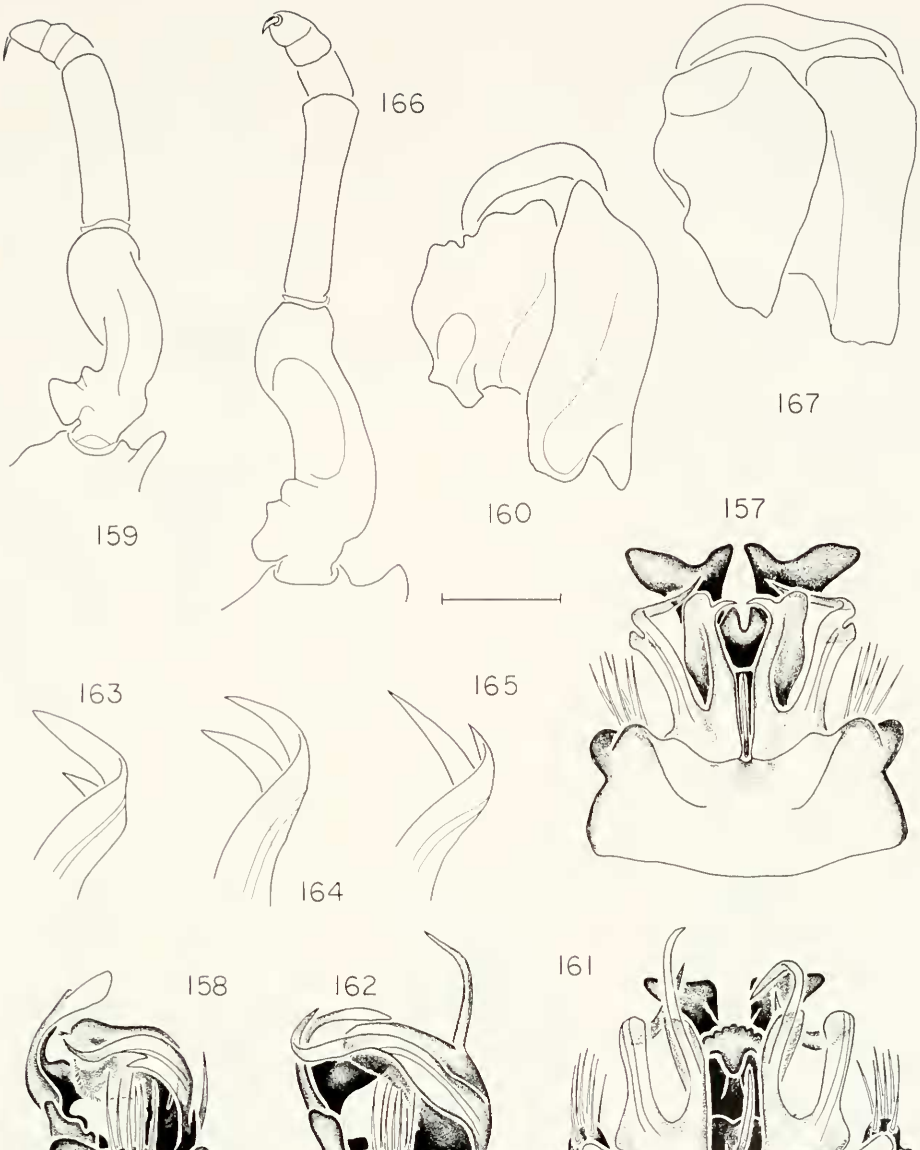


141

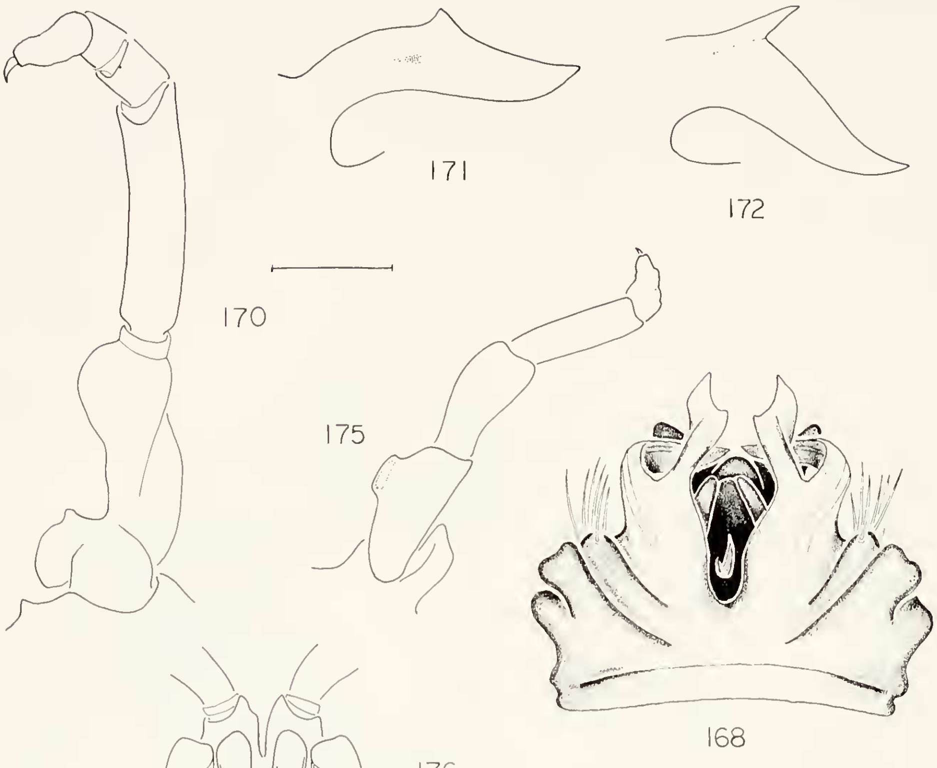
Figures 140–148. Anatomy of *Pseudotremia* spp. Fig. 140. Right cyphopod of specimen of *P. fulgida* from same locality as those shown in Figs. 138 and 139, ventral view. Figs. 141–144. *P. carterensis*. Fig. 141. Anterior gonopods, anterior view. Fig. 142. Left anterior gonopod, lateral view. Fig. 143. Right posterior gonopod, anterior view. Fig. 144. Right cyphopod, ventral view. Figs. 145–147. *P. deprehendor*. Fig. 145. Anterior gonopods, anterior view. Fig. 146. Left anterior gonopod, lateral view. Fig. 147. Right posterior gonopod, anterior view. Fig. 148. Anterior gonopods, of *P. princeps*, anterior view. Scale lines = 0.5 mm for anterior and posterior gonopods, 0.25 mm for cyphopods.



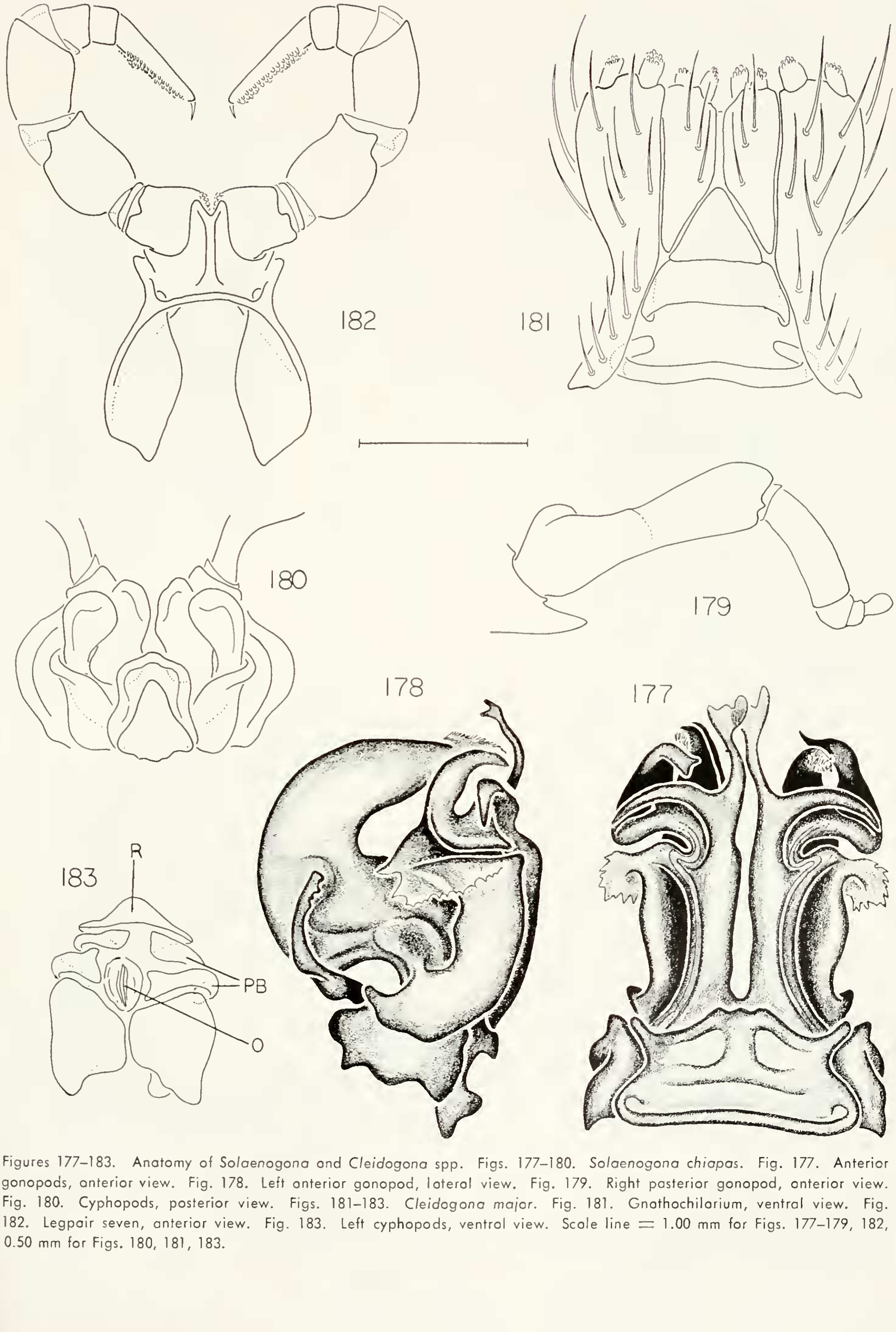
Figures 149–156. Anatomy of *Pseudotremia* spp. Figs. 149–151. *P. princeps*. Fig. 149. Left anterior gonopod, lateral view. Fig. 150. Right posterior gonopod, anterior view. Fig. 151. Right cyphopod, ventral view. Figs. 152–156. *P. tsuga*. Fig. 152. Anterior gonopods, anterior view. Fig. 153. Anterior gonopods, ventral view. Fig. 154. Left anterior gonopod, lateral view. Fig. 155. Right posterior gonopod, anterior view. Fig. 156. Right cyphopod, ventral view. Scale lines = 0.5 mm for anterior and posterior gonopods, 0.25 mm for cyphopods.



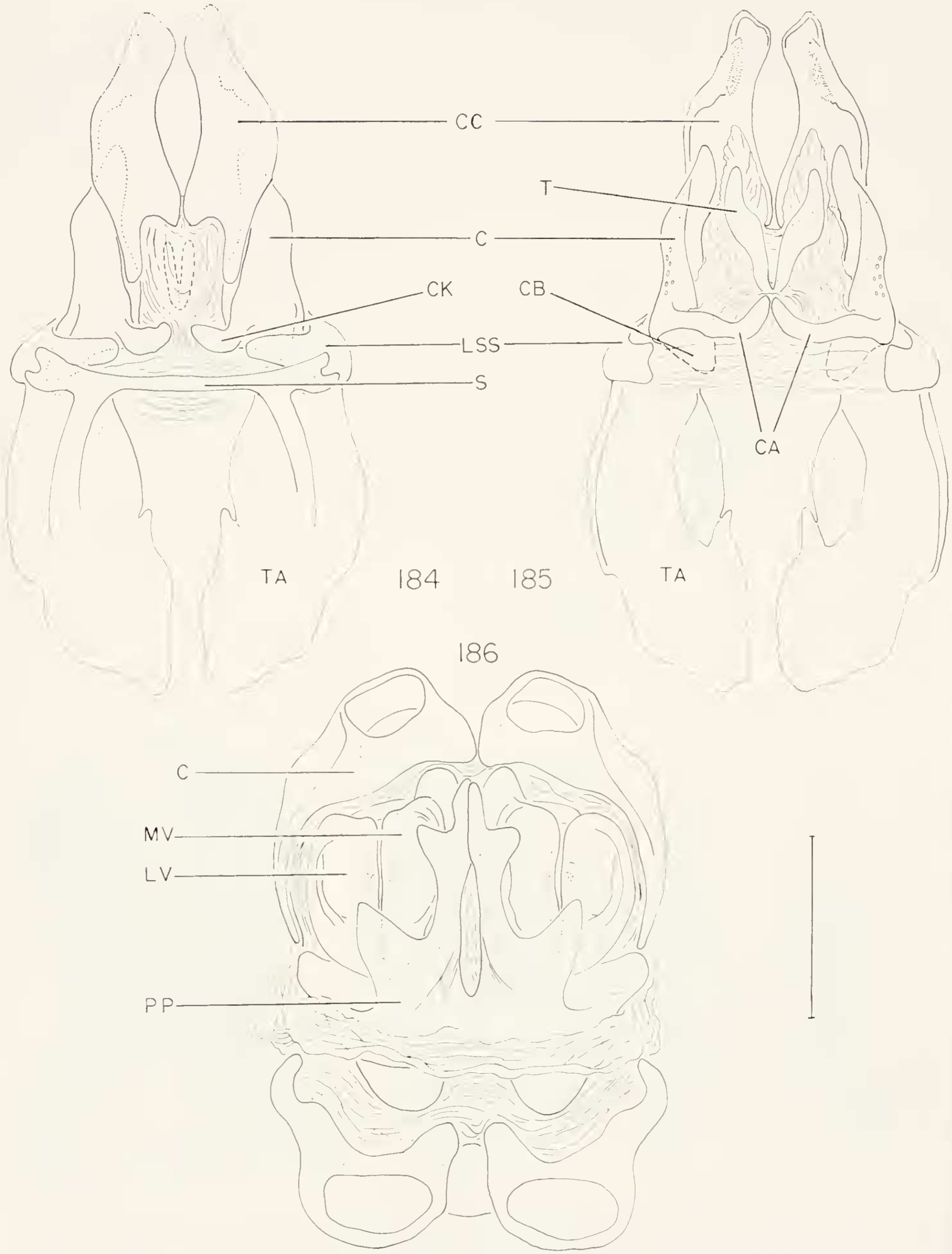
Figures 157–167. Anatomy of *Pseudotremia* spp. Figs. 157–160. *P. cavernarum*. Fig. 157. Anterior gonopods, anterior view. Fig. 158. Left anterior gonopod, lateral view. Fig. 159. Right posterior gonopod, anterior view. Fig. 160. Right cyphopod, ventral view. Figs. 161–167. *P. hobbsi*. Fig. 161. Anterior gonopods, anterior view. Fig. 162. Left anterior gonopod, lateral view. Figs. 163–165. Tips of lateral colpocoxites of gonopods, lateral view. Fig. 163. Specimen from Higgenbotham Cove. Fig. 164. Specimen from Rock Camp Cave. Fig. 165. Specimen from Laurel Creek Cove system. Fig. 166. Right posterior gonopod, anterior view. Fig. 167. Right cyphopod of specimen from Warm Springs Mtn., ventral view. Scale lines = 0.5 mm for anterior and posterior gonopods, 0.25 mm for cyphopods.



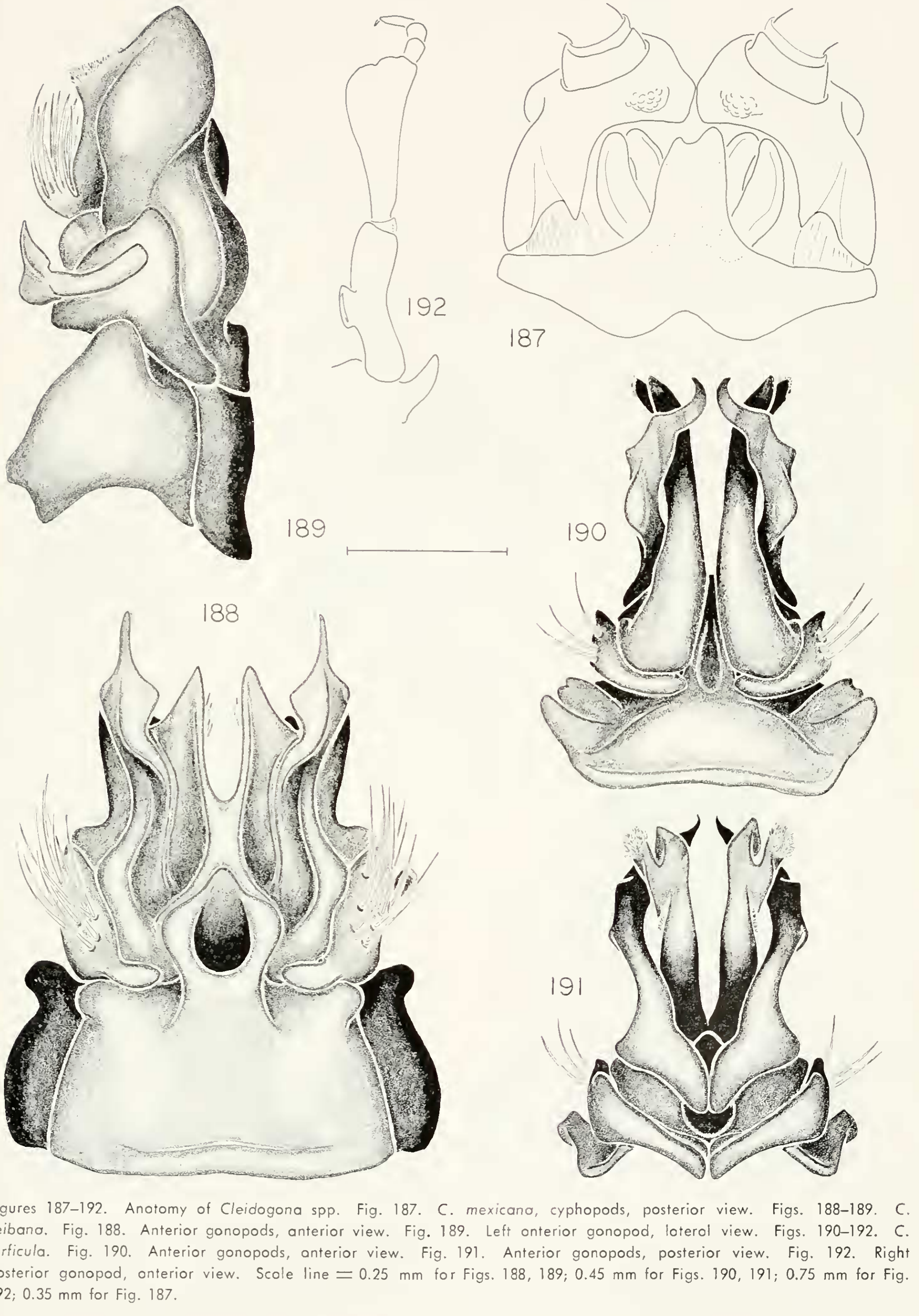
Figures 168–176. Anatomy of *Pseudotremia* and *Solaenogona* spp. Figs. 168–170. *Pseudotremia sublevis*. Fig. 168. Anterior gonopods, anterior view. Fig. 169. Left anterior gonopod, lateral view. Fig. 170. Right posterior gonopod, anterior view. Figs. 171–172. Ventral branches of lateral colpocoxites of gonopods. Fig. 171. Holotype. Fig. 172. Specimen from near Newport, Va. Figs. 173–176. *Solaenogona guatemalana*. Fig. 173. Anterior gonopods, anterior view. Fig. 174. Left anterior gonopod, lateral view. Fig. 175. Right posterior gonopod, anterior view. Fig. 176. Cyphopods, posterior view. Scale lines = 0.5 mm for anterior and posterior gonopods, 0.25 mm for cyphopods.



Figures 177–183. Anatomy of *Solaenogona* and *Cleidogona* spp. Figs. 177–180. *Solaenogona chiapas*. Fig. 177. Anterior gonopods, anterior view. Fig. 178. Left anterior gonopod, lateral view. Fig. 179. Right posterior gonopod, anterior view. Fig. 180. Cyphopods, posterior view. Figs. 181–183. *Cleidogona major*. Fig. 181. Gnathochilarium, ventral view. Fig. 182. Legpair seven, anterior view. Fig. 183. Left cyphopods, ventral view. Scale line = 1.00 mm for Figs. 177–179, 182, 0.50 mm for Figs. 180, 181, 183.

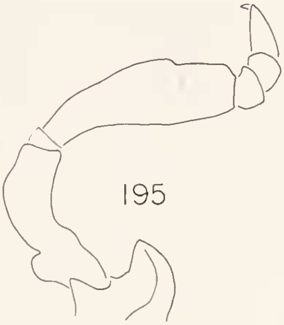


Figures 184–186. Anatomy of *Cleidogona major*. Fig. 184. Anterior gonopods, anterior view. Fig. 185. Anterior gonopods, posterior view. Fig. 186. Cyphopods, ventroposterior view. Scale line = 0.5 mm.



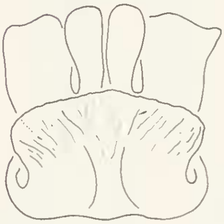
Figures 187–192. Anatomy of *Cleidogona* spp. Fig. 187. *C. mexicana*, cyphopods, posterior view. Figs. 188–189. *C. ceibana*. Fig. 188. Anterior gonopods, anterior view. Fig. 189. Left anterior gonopod, lateral view. Figs. 190–192. *C. forficula*. Fig. 190. Anterior gonopods, anterior view. Fig. 191. Anterior gonopods, posterior view. Fig. 192. Right posterior gonopod, anterior view. Scale line = 0.25 mm for Figs. 188, 189; 0.45 mm for Figs. 190, 191; 0.75 mm for Fig. 192; 0.35 mm for Fig. 187.

195

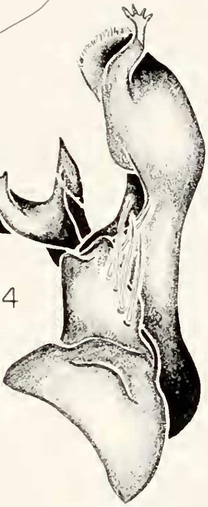


199

196

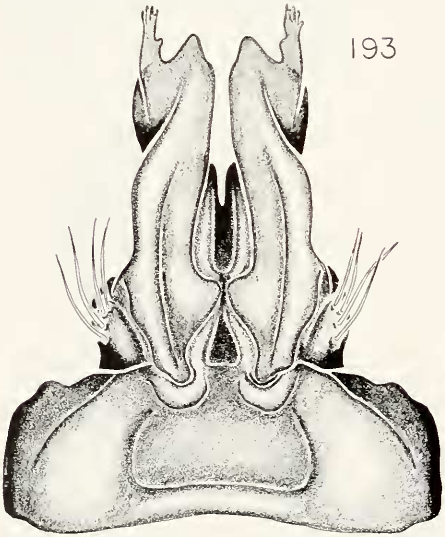


194

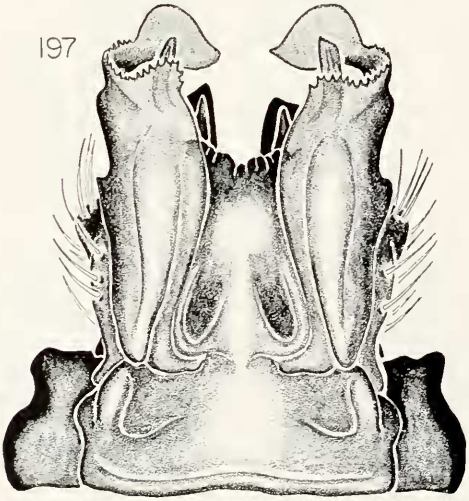


198

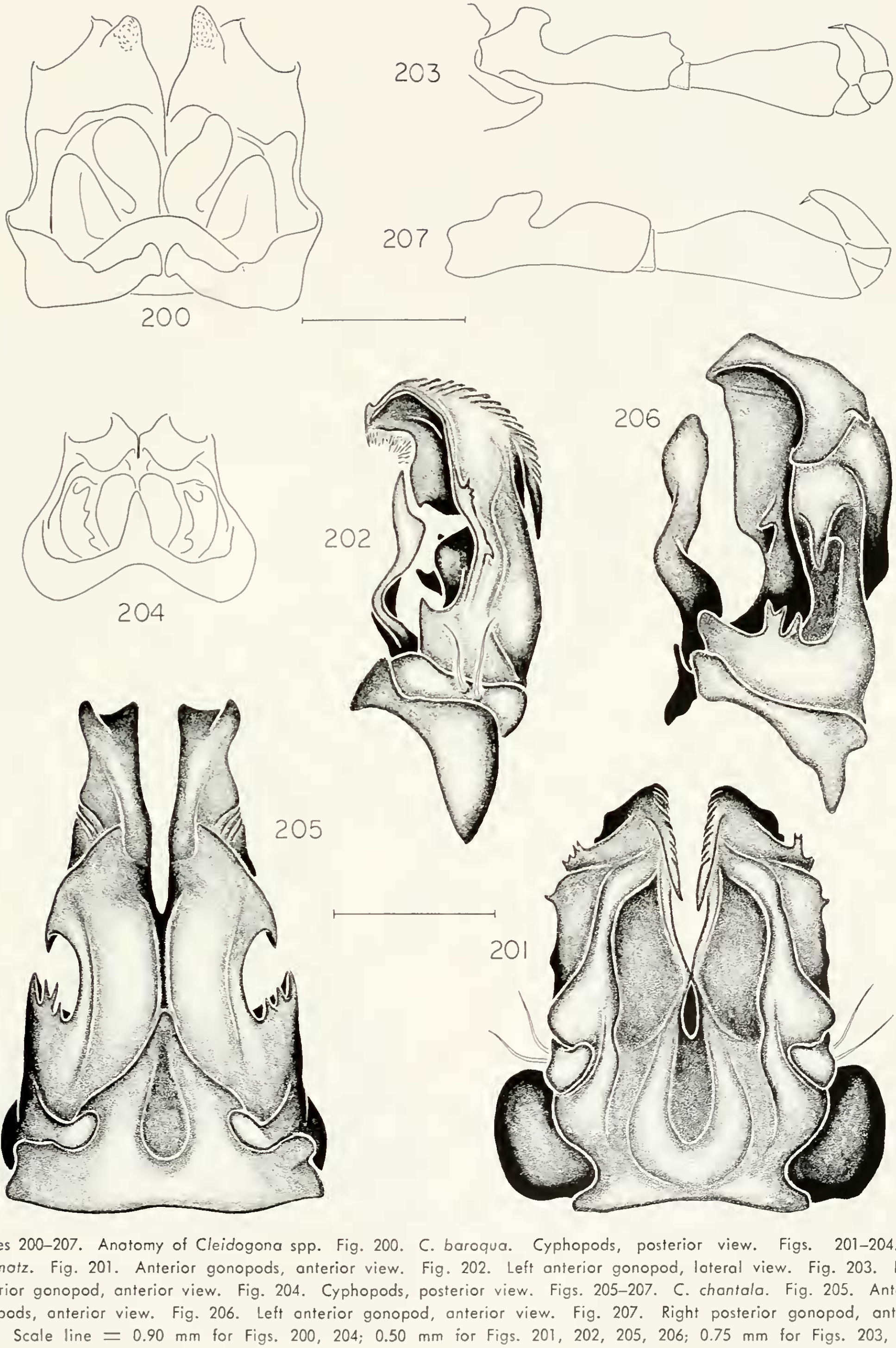
193



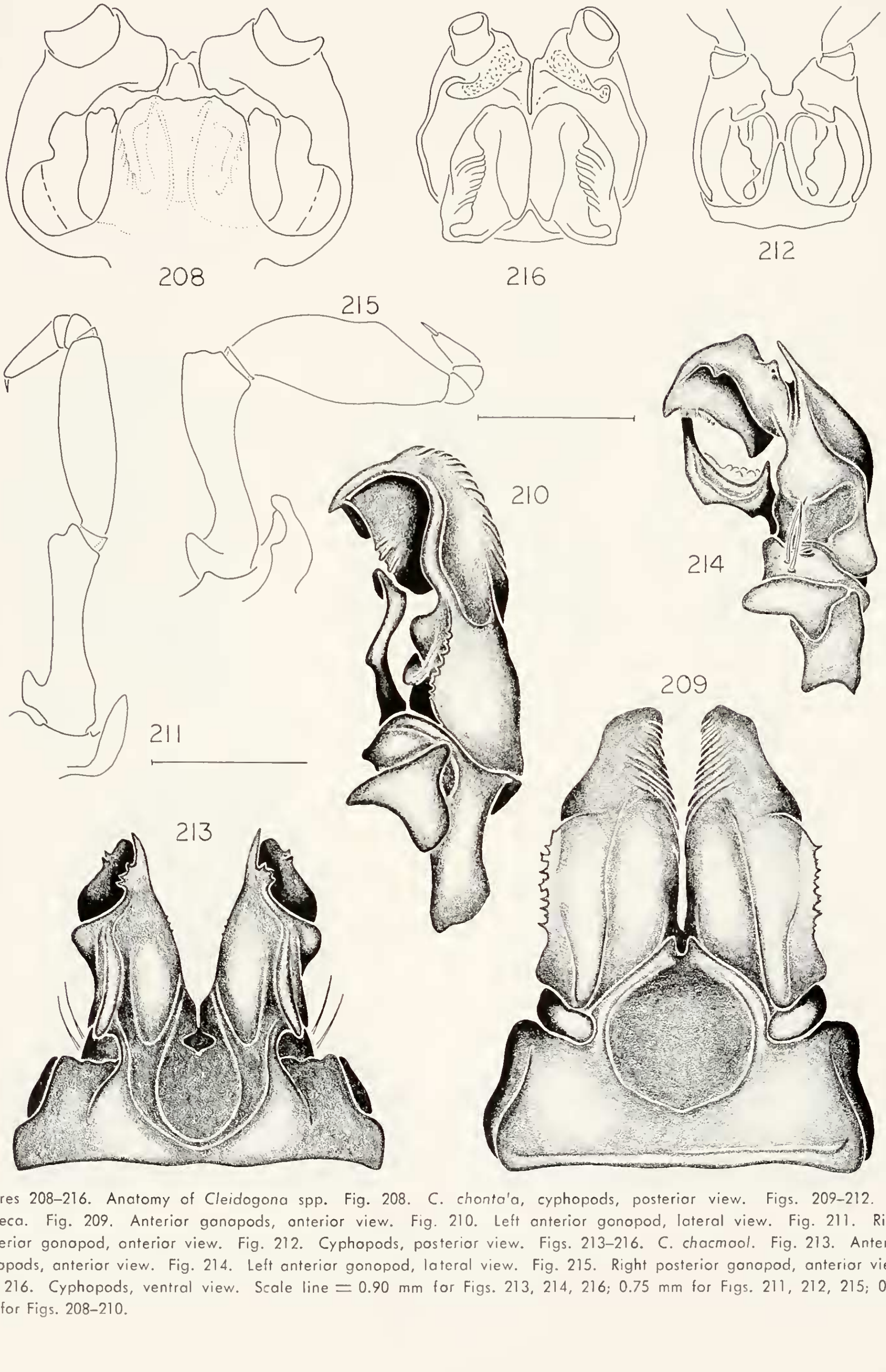
197



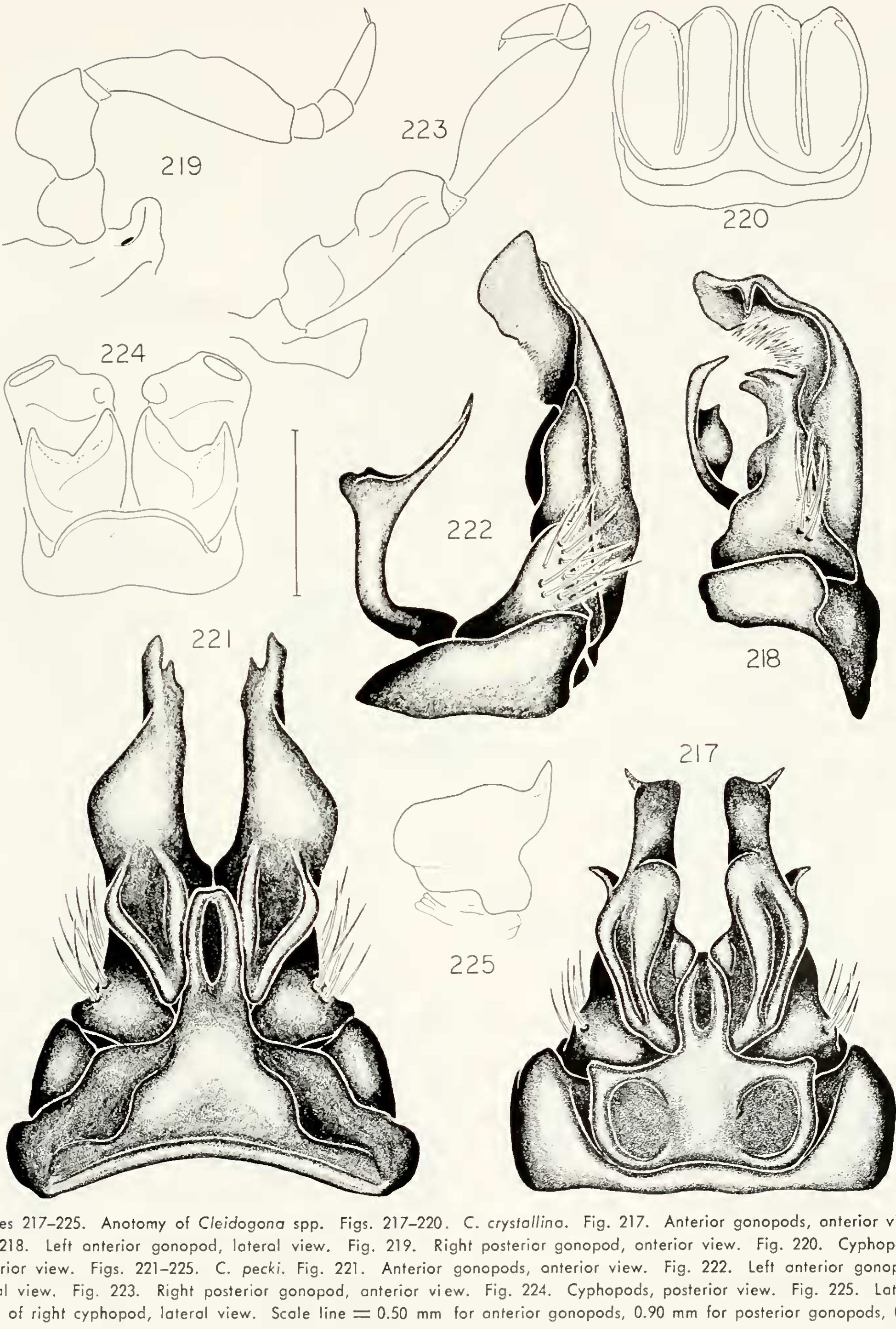
Figures 193–199. Anatomy of *Cleidogona* spp. Figs. 193–196. *C. crucis.* Fig. 193. Anterior gonopods, anterior view. Fig. 194. Left anterior gonopod, lateral view. Fig. 195. Right posterior gonopod, anterior view. Fig. 196. Cyphopods, posterior view. Figs. 197–199. *C. baroqua.* Fig. 197. Anterior gonopods, anterior view. Fig. 198. Left anterior gonopod, lateral view. Fig. 199. Right posterior gonopod, anterior view. Scale line = 0.50 mm for Figs. 193, 194; 0.35 mm for Fig. 196; 0.90 mm for Figs. 195, 197–199.



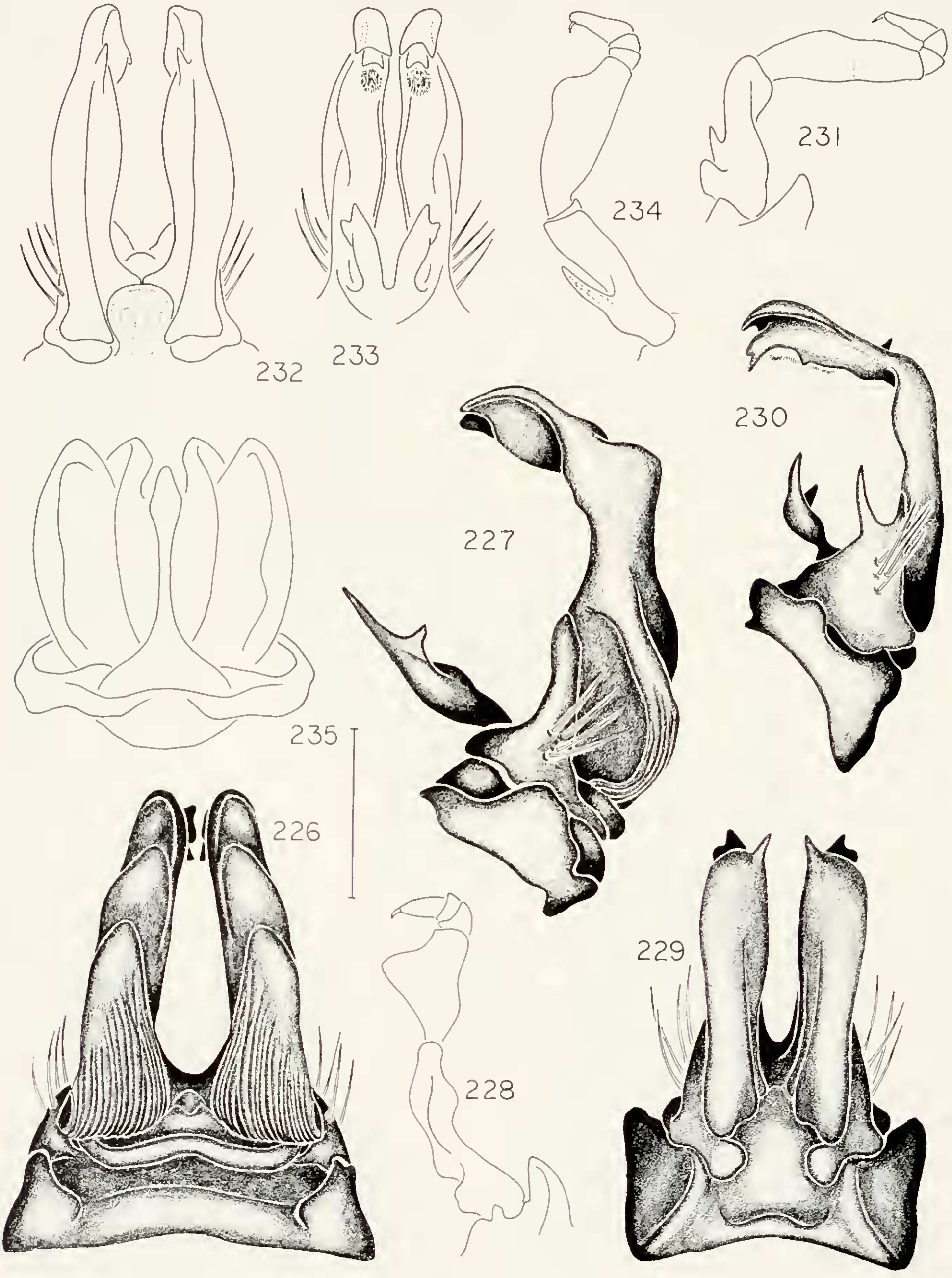
Figures 200–207. Anatomy of *Cleidogona* spp. Fig. 200. *C. baroqua*. Cyphopods, posterior view. Figs. 201–204. *C. gucumatz*. Fig. 201. Anterior gonopods, anterior view. Fig. 202. Left anterior gonopod, lateral view. Fig. 203. Right posterior gonopod, anterior view. Fig. 204. Cyphopods, posterior view. Figs. 205–207. *C. chantala*. Fig. 205. Anterior gonopods, anterior view. Fig. 206. Left anterior gonopod, anterior view. Fig. 207. Right posterior gonopod, anterior view. Scale line = 0.90 mm for Figs. 200, 204; 0.50 mm for Figs. 201, 202, 205, 206; 0.75 mm for Figs. 203, 207.



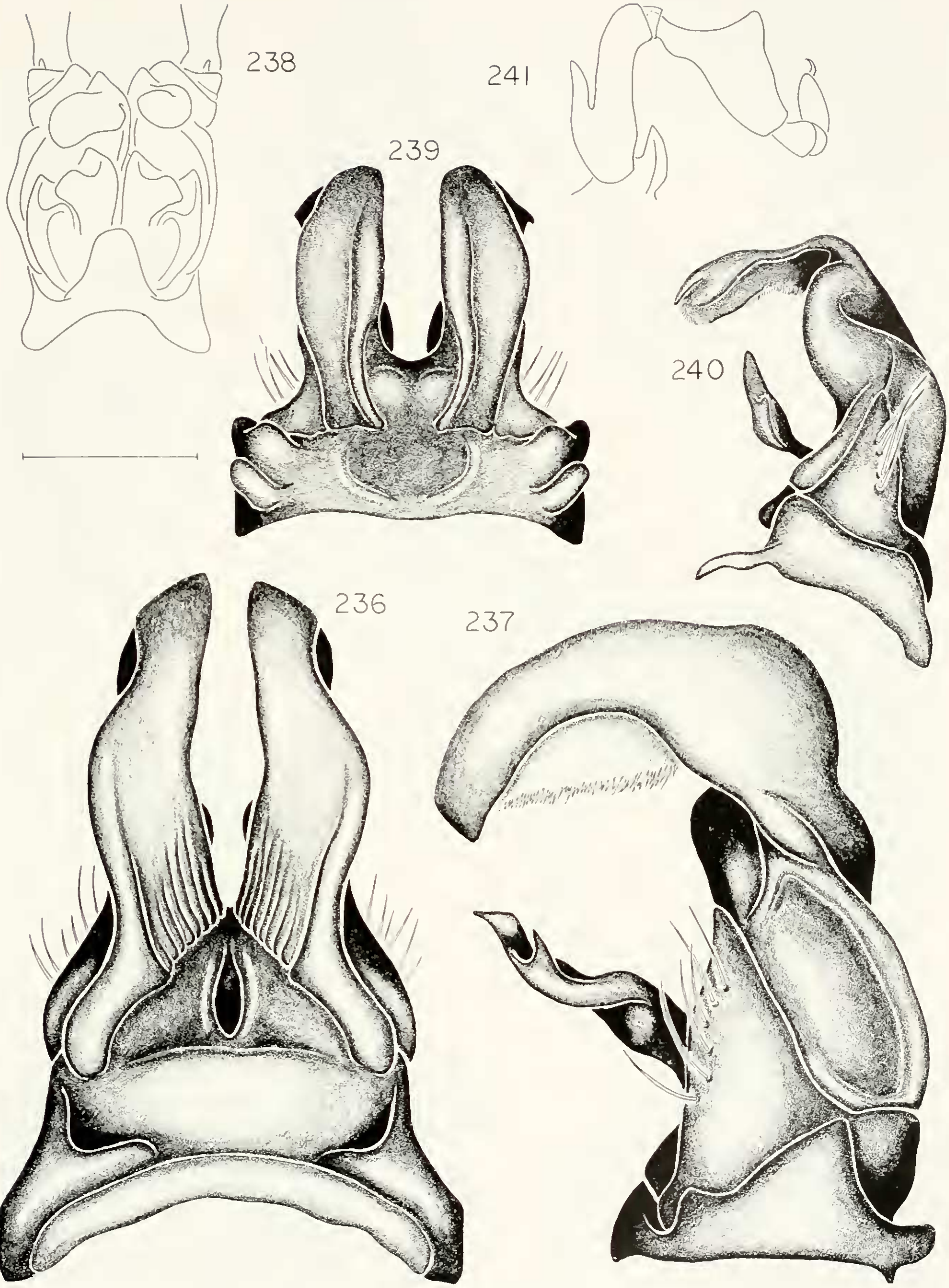
Figures 208–216. Anatomy of *Cleidogona* spp. Fig. 208. *C. chonta'a*, cyphopods, posterior view. Figs. 209–212. *C. mixteca*. Fig. 209. Anterior gonopods, anterior view. Fig. 210. Left anterior gonopod, lateral view. Fig. 211. Right posterior gonopod, anterior view. Fig. 212. Cyphopods, posterior view. Figs. 213–216. *C. chacmool*. Fig. 213. Anterior gonopods, anterior view. Fig. 214. Left anterior gonopod, lateral view. Fig. 215. Right posterior gonopod, anterior view. Fig. 216. Cyphopods, ventral view. Scale line = 0.90 mm for Figs. 213, 214, 216; 0.75 mm for Figs. 211, 212, 215; 0.45 mm for Figs. 208–210.



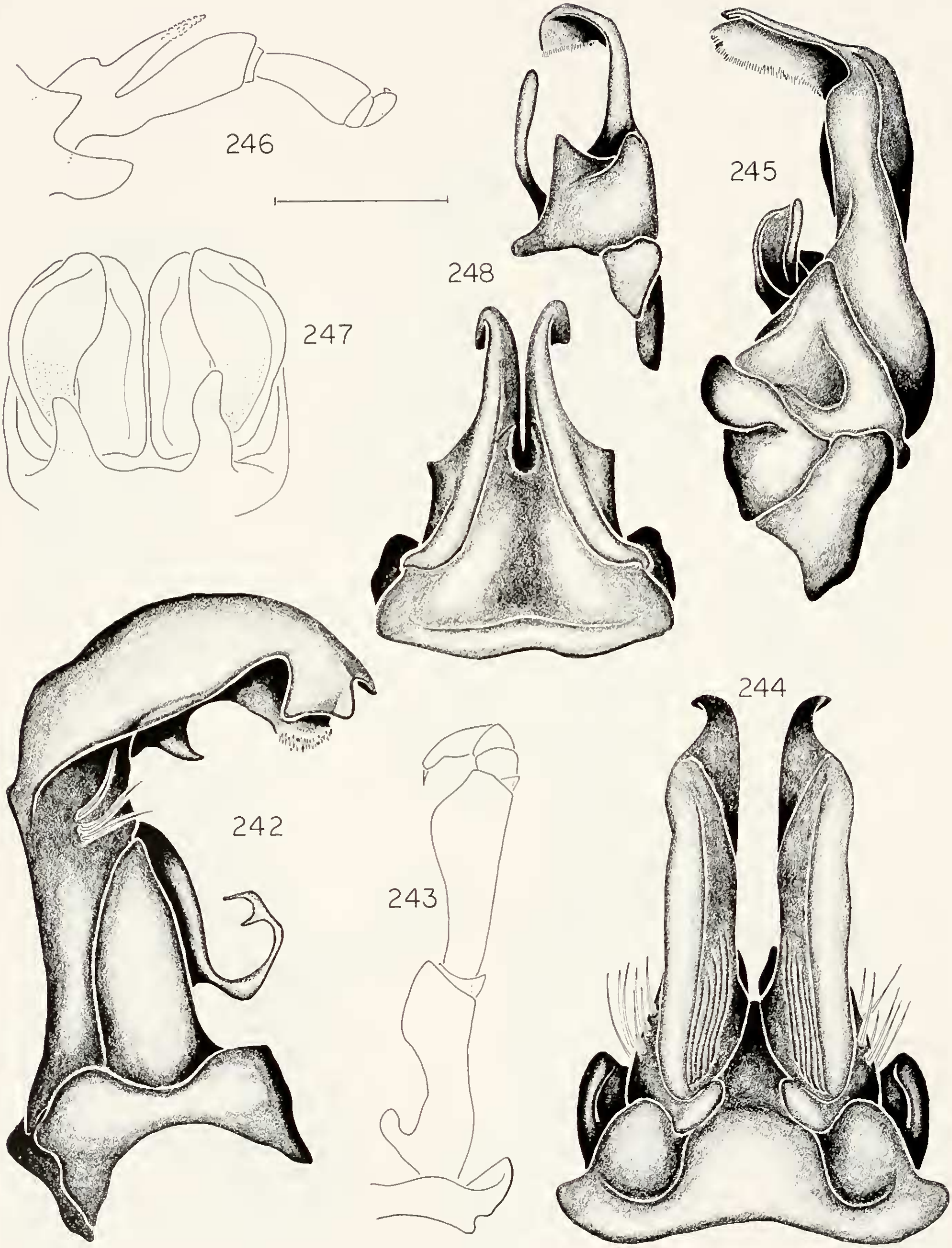
Figures 217–225. Anatomy of *Cleidogona* spp. Figs. 217–220. *C. crystallina*. Fig. 217. Anterior gonopods, anterior view. Fig. 218. Left anterior gonopod, lateral view. Fig. 219. Right posterior gonopod, anterior view. Fig. 220. Cyphopods, posterior view. Figs. 221–225. *C. pecki*. Fig. 221. Anterior gonopods, anterior view. Fig. 222. Left anterior gonopod, lateral view. Fig. 223. Right posterior gonopod, anterior view. Fig. 224. Cyphopods, posterior view. Fig. 225. Lateral valve of right cyphopod, lateral view. Scale line = 0.50 mm for anterior gonopods, 0.90 mm for posterior gonopods, 0.35 mm for cyphopods.



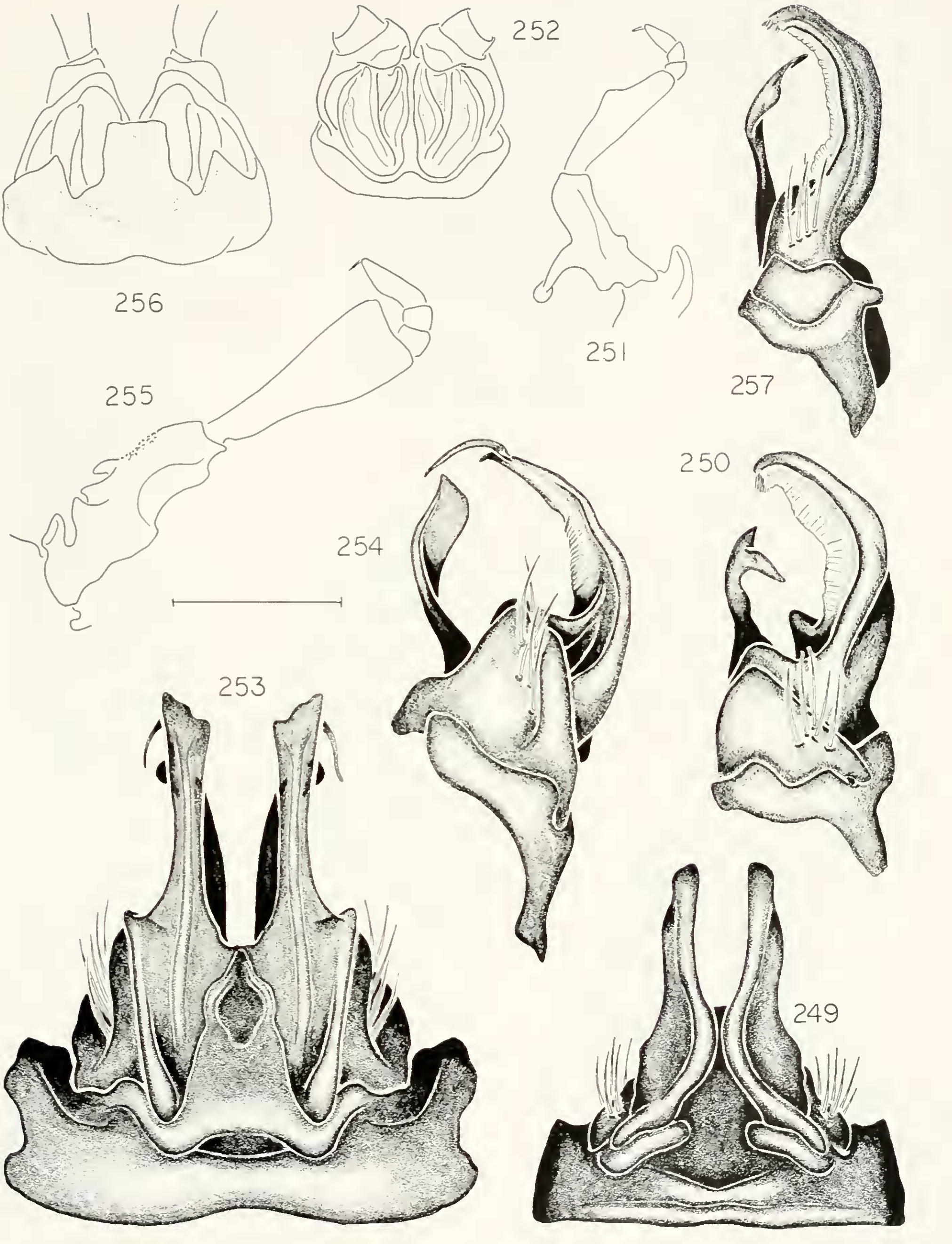
Figures 226–235. Anatomy of *Cleidogona* spp. Figs. 226–228. *C. maculata*. Fig. 226. Anterior gonopods, anterior view. Fig. 227. Left anterior gonopod, lateral view. Fig. 228. Right posterior gonopod, anterior view. Figs. 229–231. *C. tizoc*. Fig. 229. Anterior gonopods, anterior view. Fig. 230. Left anterior gonopod, lateral view. Fig. 231. Posterior gonopod, anterior view. Figs. 232–235. *C. zimapaniensis*. Fig. 232. Anterior gonopods, anterior view. Fig. 233. Anterior gonopods, posterior view. Fig. 234. Right posterior gonopod, anterior view. Fig. 235. Cyphopods, posterior view. Scale line = 0.50 mm for Figs. 226–230; 0.90 mm for Fig. 231; 0.45 mm for Figs. 232–235.



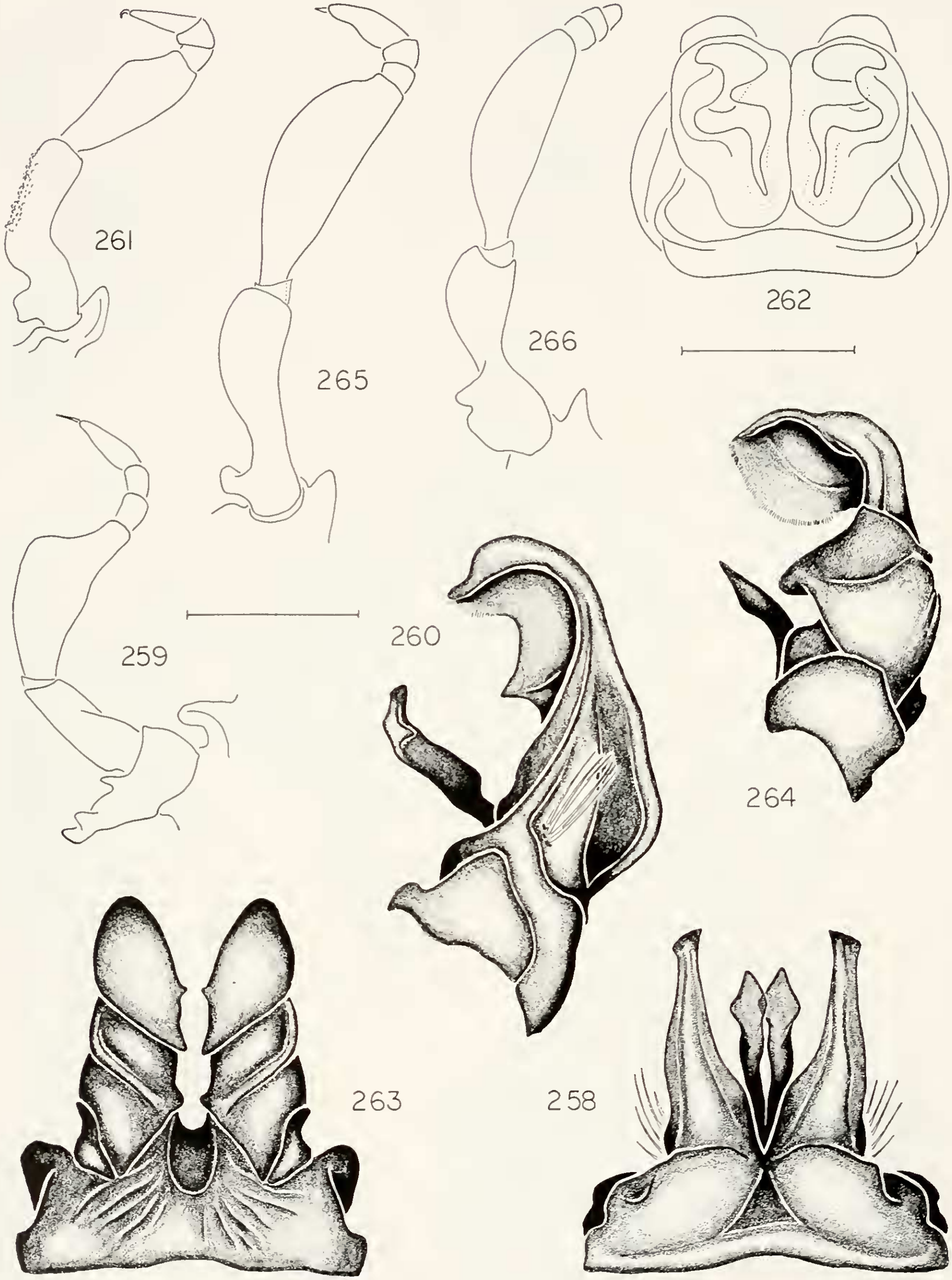
Figures 236–241. Anatomy of *Cleidogona* spp. Figs. 236–238. *C. camazotz*. Fig. 236. Anterior gonopods, anterior view. Fig. 237. Left anterior gonopod, lateral view. Fig. 238. Cyphopods, posterior view. Figs. 239–241. *C. mayapec*. Fig. 239. Anterior gonopods, anterior view. Fig. 240. Left anterior gonopod, lateral view. Fig. 241. Right posterior gonopod, anterior view. Scale line = 0.50 mm for Figs. 236, 237; 1.00 mm for Fig. 238; 0.45 mm for Figs. 239, 240; 0.90 mm for Fig. 241.



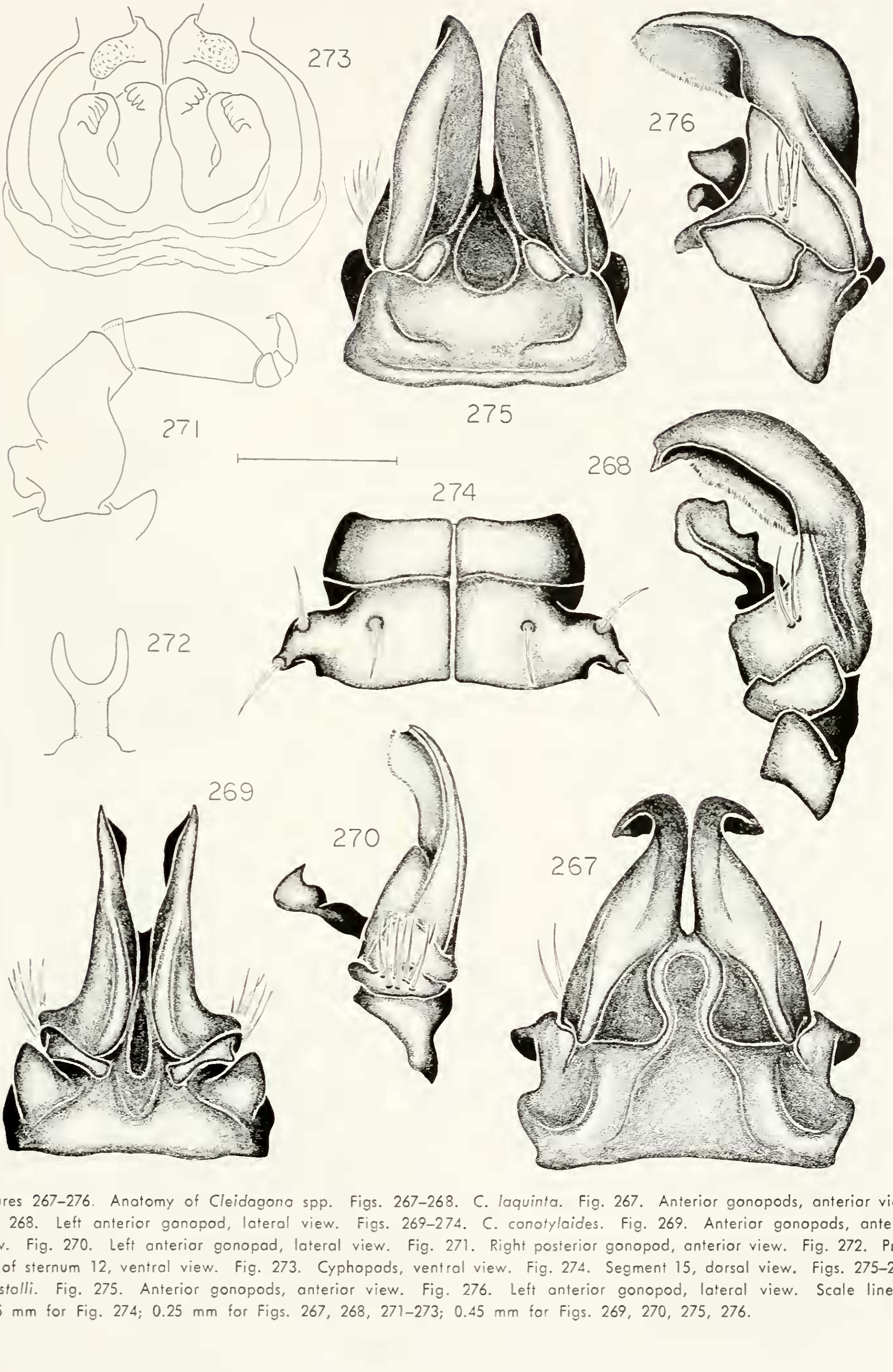
Figures 242–248. Anatomy of *Cleidogona* spp. Figs. 242–243. *C. xolotl*. Fig. 242. Right anterior gonopod, lateral view. Fig. 243. Right posterior gonopod, anterior view. Figs. 244–247. *C. bacillipus*. Fig. 244. Anterior gonopods, anterior view. Fig. 245. Left anterior gonopod, lateral view. Fig. 246. Right posterior gonopod, anterior view. Fig. 247. Cyphopods, posterior view. Fig. 248. Anterior gonopods of *C. godmani*, anterior view below, lateral view of left gonopod above. Scale line = 0.25 mm for all anterior gonopods; 0.75 mm for Fig. 246; 0.45 mm for Fig. 243; 0.35 mm for Fig. 247.



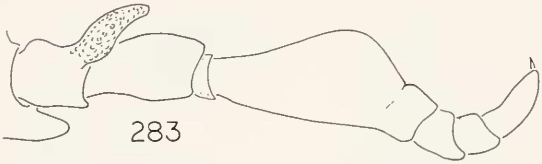
Figures 249–257. Anatomy of *Cleidogona* spp. Figs. 249–252. *C. tequila.* Fig. 249. Anterior gonopods, anterior view. Fig. 250. Left anterior gonopod, lateral view. Fig. 251. Right posterior gonopod, anterior view. Fig. 252. Cyphopods, ventral view. Figs. 253–256. *C. hauatla.* Fig. 253. Anterior gonopods, anterior view. Fig. 254. Left anterior gonopod, lateral view. Fig. 255. Right posterior gonopod, anterior view. Fig. 256. Cyphopods, posterior view. Fig. 257. *C. totonaca*, left anterior gonopod, lateral view. Scale line = 0.50 mm for Figs. 253, 254, 257; 0.45 mm for Figs. 249, 250; 0.90 mm for posterior gonopods and cyphopods.



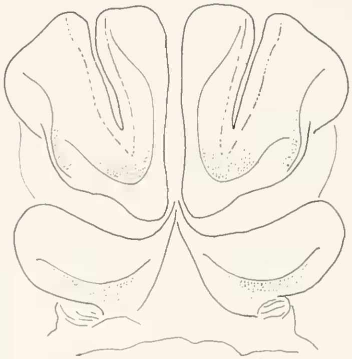
Figures 258–266. Anatomy of *Cleidogona* spp. Figs. 258–259. *C. totonaca.* Fig. 258. Anterior gonopods, anterior view. Fig. 259. Right posterior gonopod, anterior view. Figs. 260–262. *C. rafaela.* Fig. 260. Left anterior gonopod, lateral view. Fig. 261. Right posterior gonopod, anterior view. Fig. 262. Cyphopods, posterior-ventral view. Figs. 263–265. *C. zapoteca.* Fig. 263. Anterior gonopods, anterior view. Fig. 264. Left anterior gonopod, lateral view. Fig. 265. Right posterior gonopod, anterior view. Fig. 266. *C. laquinta*, right posterior gonopod, anterior view. Scale lines = 0.45 mm for Figs. 262–264; 0.75 mm for posterior gonopods; 0.50 mm for Fig. 258; 0.35 mm for Fig. 260.



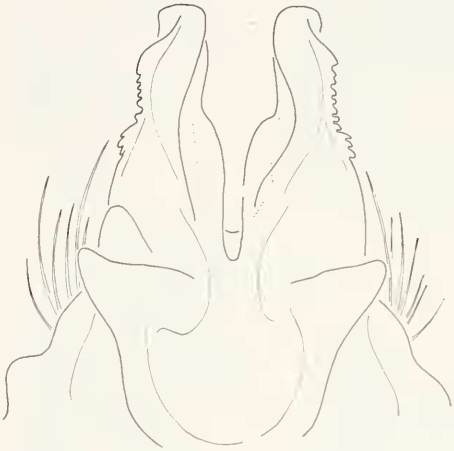
Figures 267–276. Anatomy of *Cleidagona* spp. Figs. 267–268. *C. laquinta.* Fig. 267. Anterior gonopods, anterior view. Fig. 268. Left anterior gonopod, lateral view. Figs. 269–274. *C. conotylaides.* Fig. 269. Anterior gonopods, anterior view. Fig. 270. Left anterior gonopod, lateral view. Fig. 271. Right posterior gonopod, anterior view. Fig. 272. Process of sternum 12, ventral view. Fig. 273. Cyphopods, ventral view. Fig. 274. Segment 15, dorsal view. Figs. 275–276. *C. stolli.* Fig. 275. Anterior gonopods, anterior view. Fig. 276. Left anterior gonopod, lateral view. Scale line = 0.75 mm for Fig. 274; 0.25 mm for Figs. 267, 268, 271–273; 0.45 mm for Figs. 269, 270, 275, 276.



283

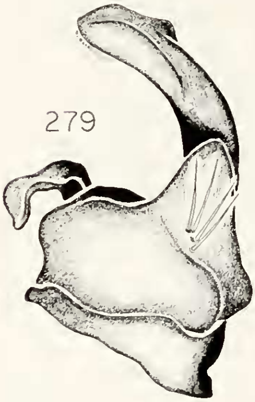


277



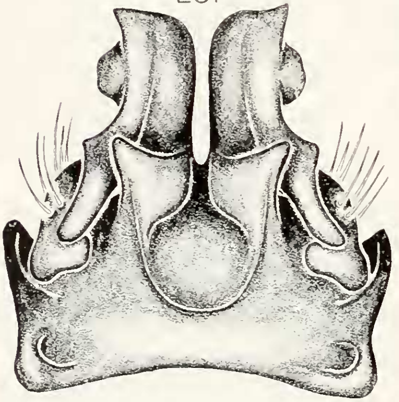
284

280

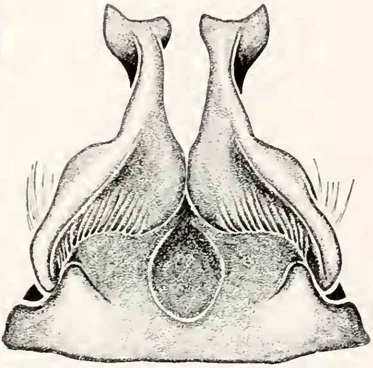


279

282

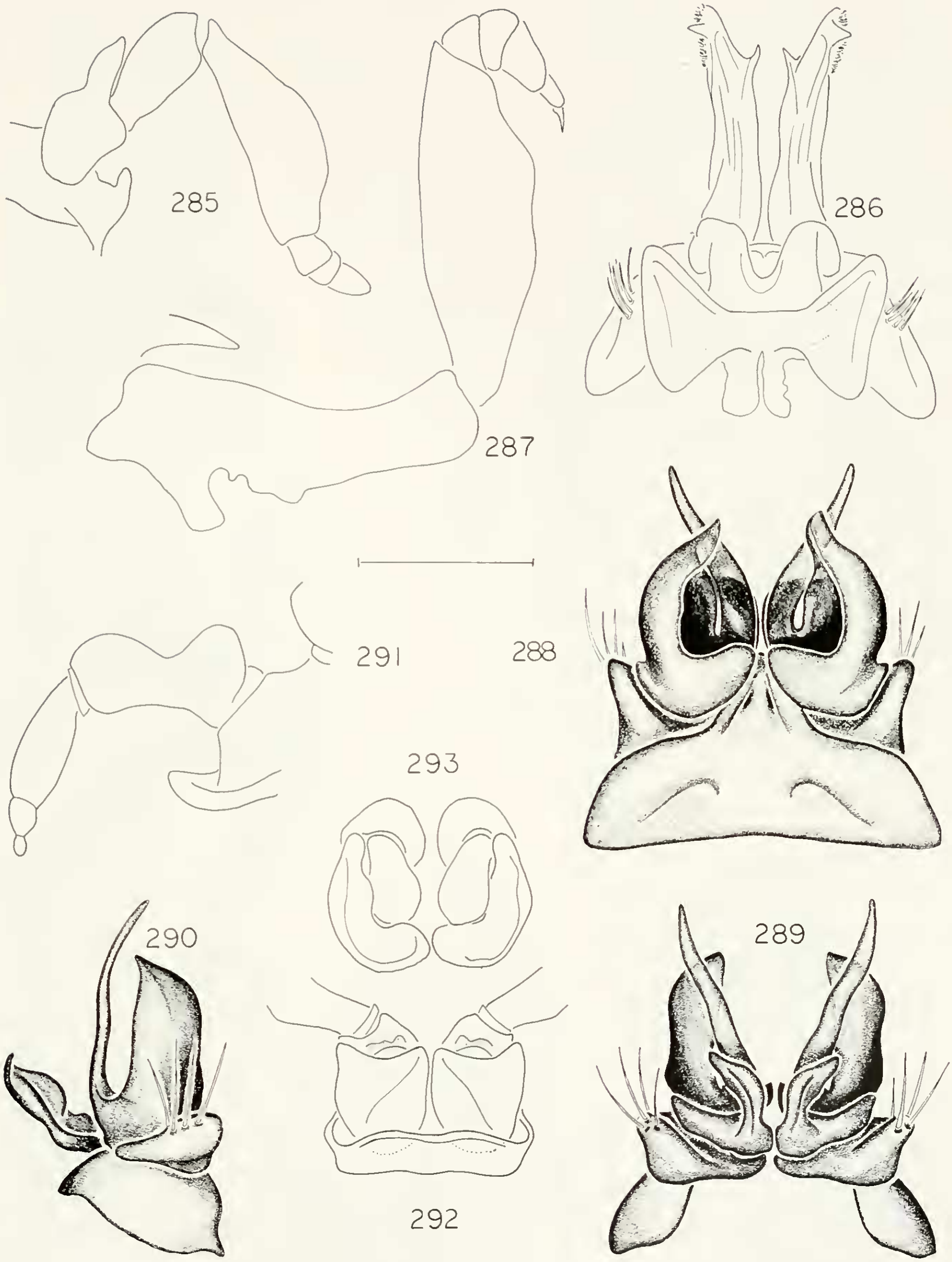


281

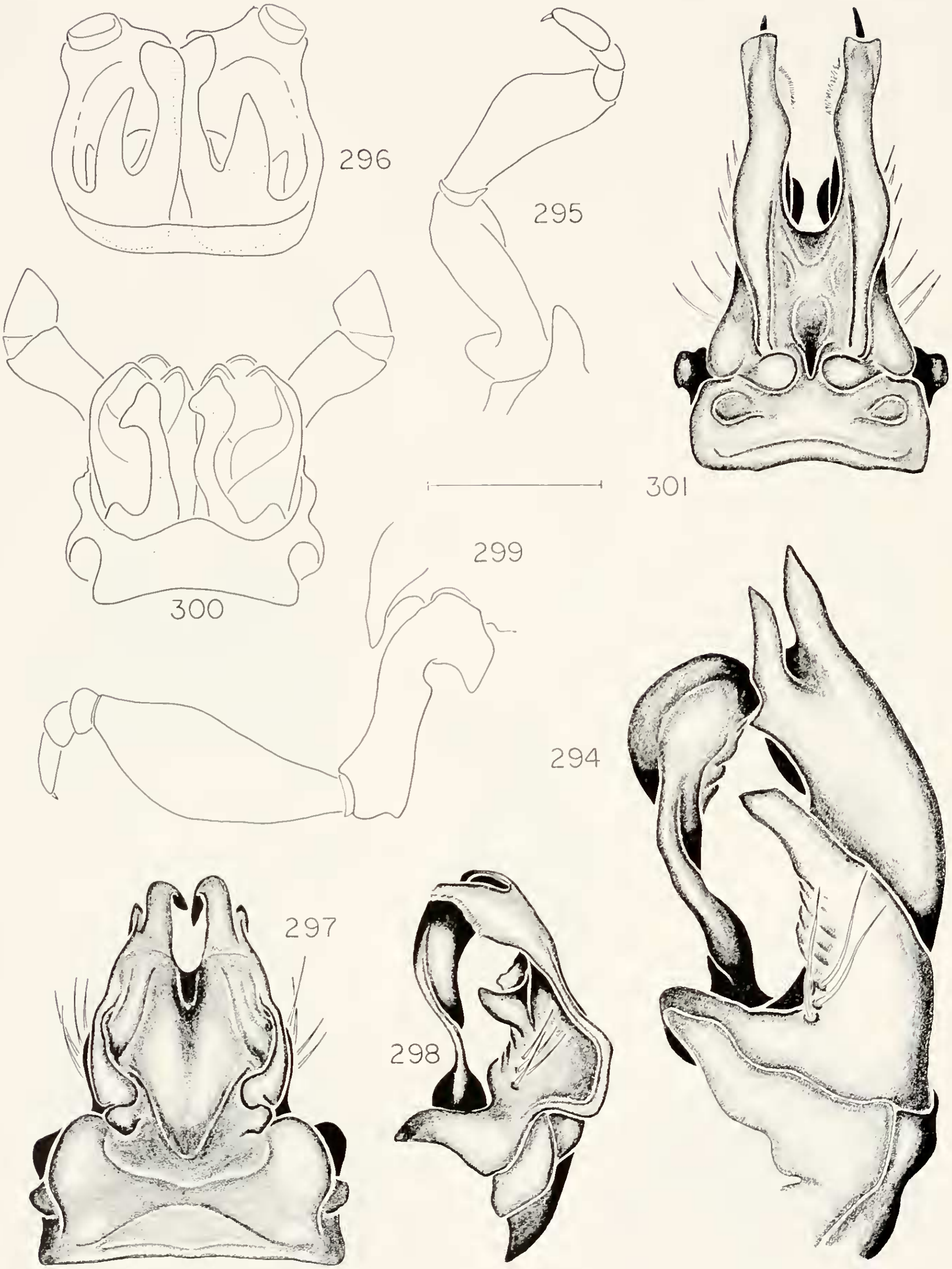


278

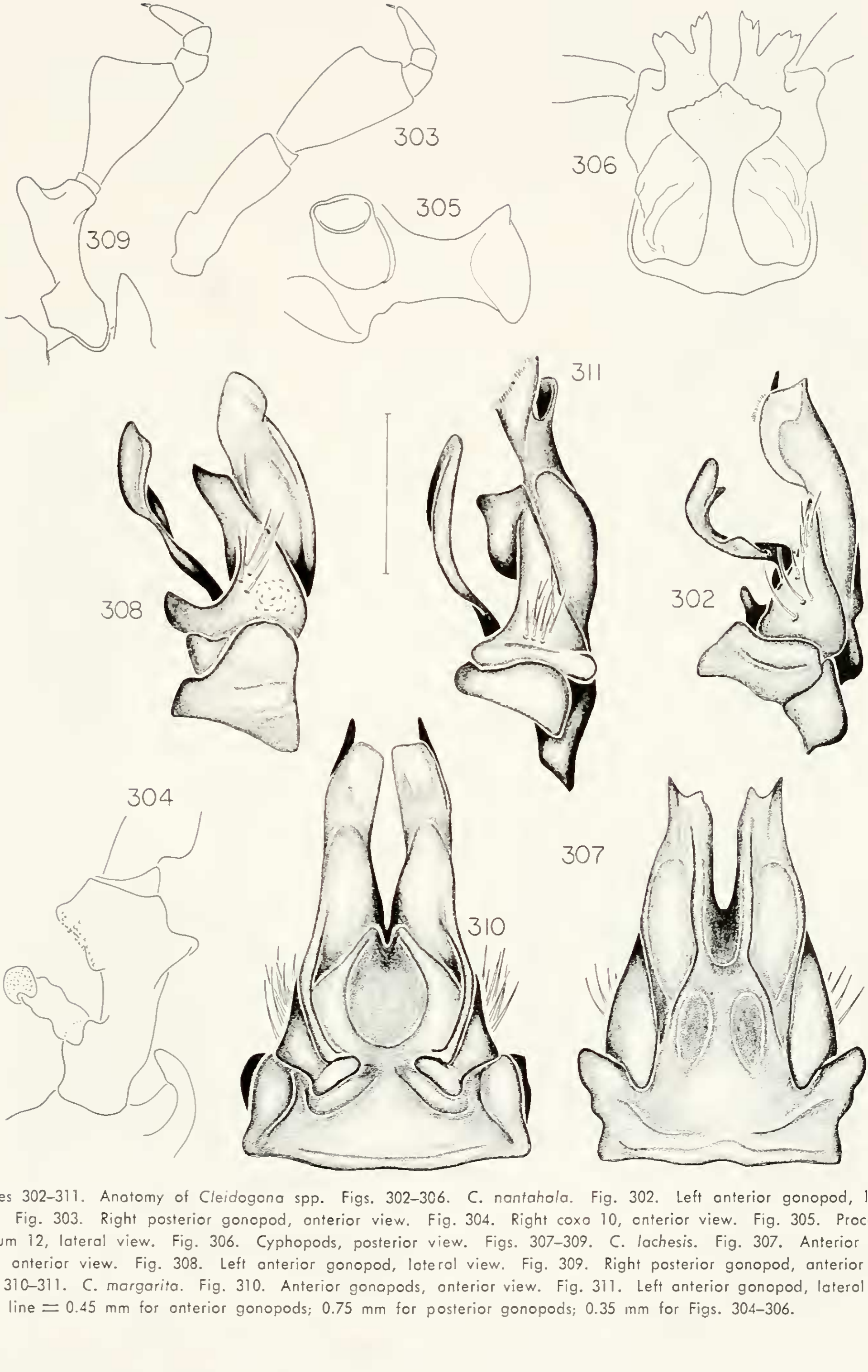
Figures 277–284. Anatomy of *Cleidogona* spp. Fig. 277. *C. stolli*, cyphopods, posterior view. Figs. 278–280. *C. decurva*. Fig. 278. Anterior gonopods, anterior view. Fig. 279. Left anterior gonopod, lateral view. Fig. 280. Right posterior gonopod, anterior view. Figs. 281–283. *C. atoyaca*. Fig. 281. Anterior gonopods, anterior view. Fig. 282. Left anterior gonopod, lateral view. Fig. 283. Right posterior gonopod, anterior view. Fig. 284. *C. minutissima*, anterior gonopods, anterior view. Scale line = 0.25 mm for Figs. 277, 281, 282; 0.45 mm for Figs. 278–280; 0.35 mm for Fig. 283; 0.10 mm for Fig. 284.



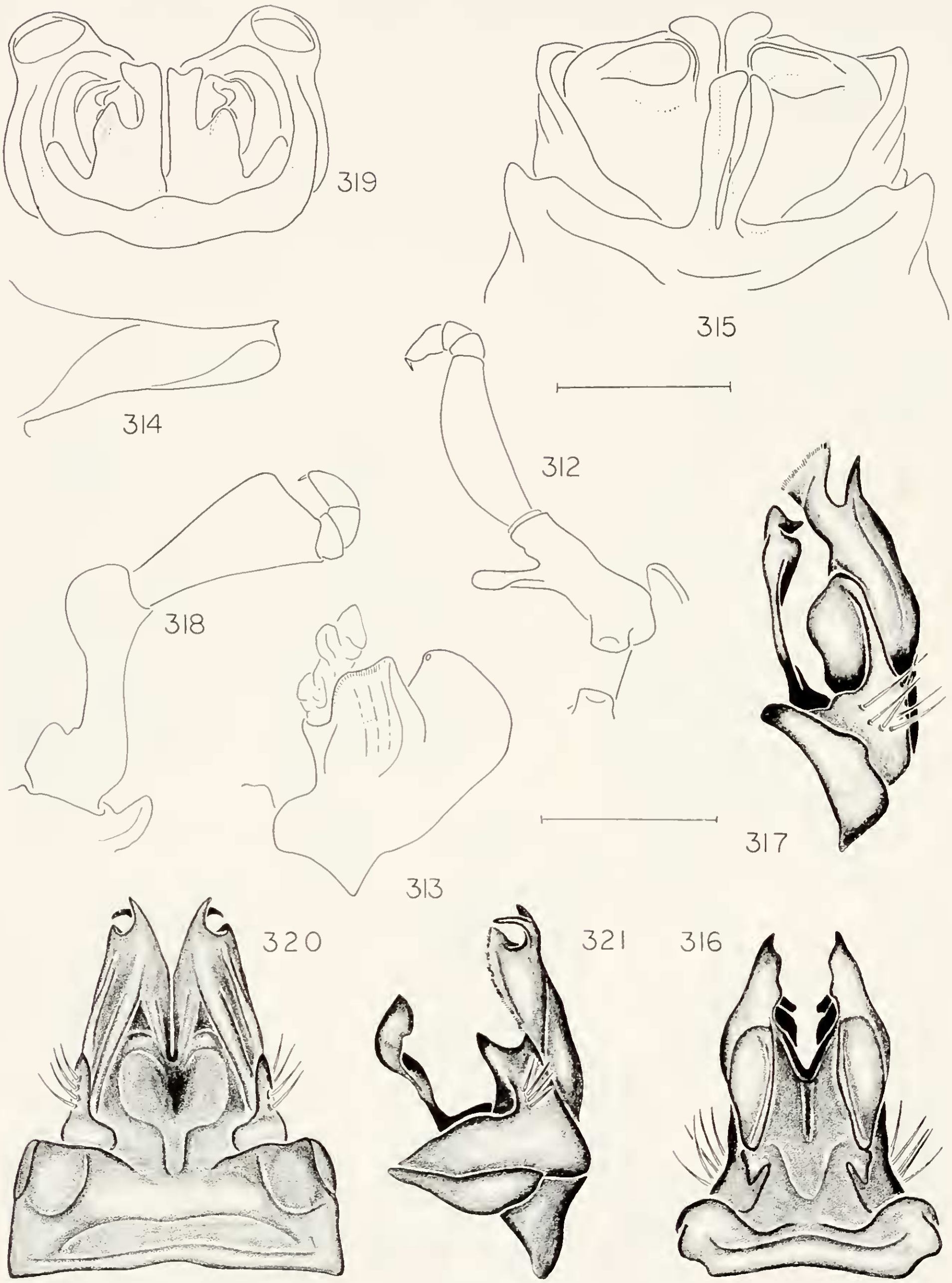
Figures 285–293. Anatomy of *Cleidogona* spp. Fig. 285. *C. minutissima*, right posterior gonopod, anterior view. Figs. 286–287. *C. mirabilis*. Fig. 286. Anterior gonopods, posterior (?) view. Fig. 287. Left posterior gonopod, anterior view. Figs. 288–293. *C. chisosi*. Fig. 288. Anterior gonopods, anterior view. Fig. 289. Anterior gonopods, posterior view. Fig. 290. Left anterior gonopod, lateral view. Fig. 291. Left posterior gonopod, anterior view. Fig. 292. Cyphopods, posterior view. Fig. 293. Cyphopods, ventral view. Scale line = 0.10 mm for Figs. 285–287, 0.25 mm for Figs. 288–293.



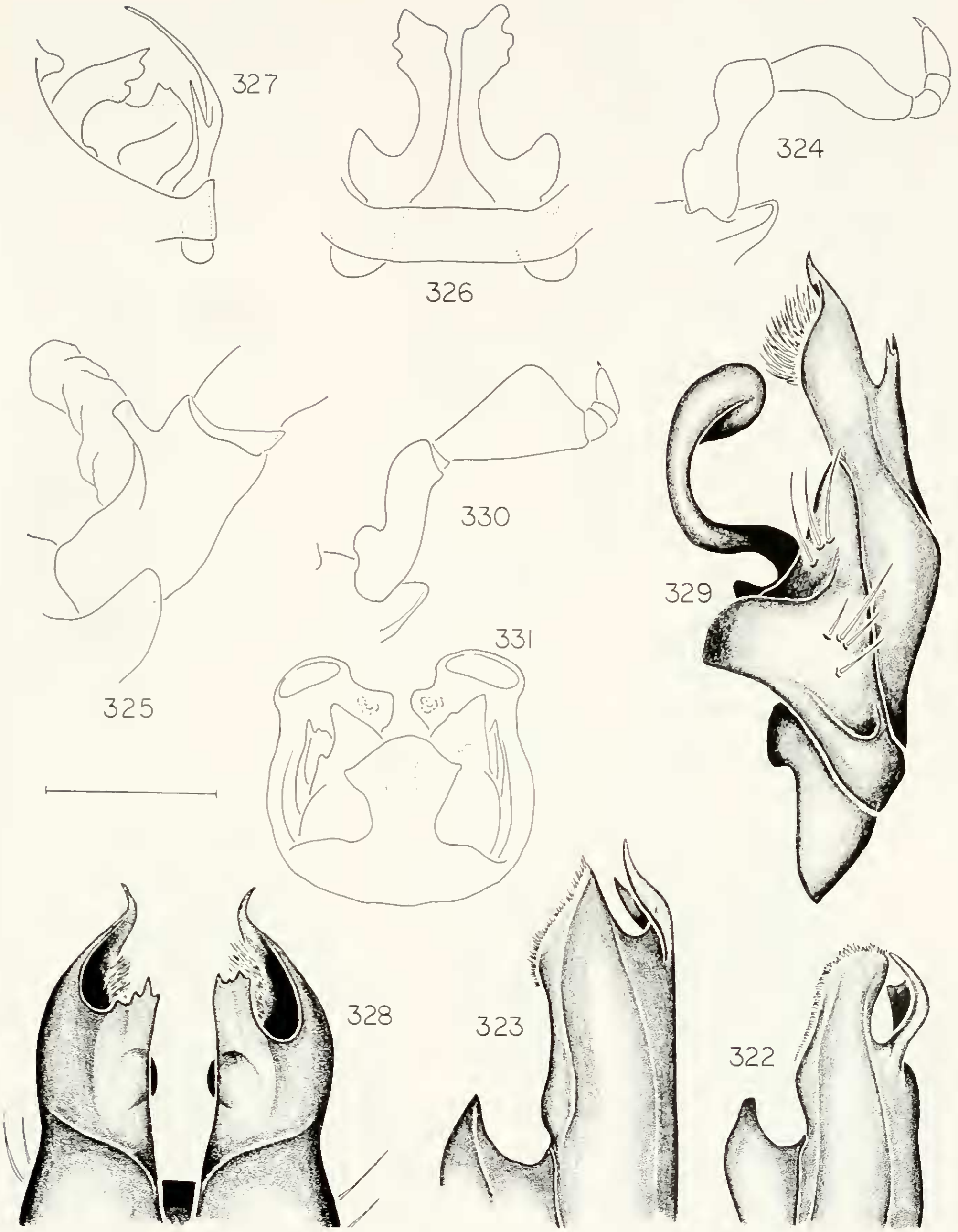
Figures 294–301. Anatomy of *Cleidogona* spp. Figs. 294–296. *C. major*. Fig. 294. Left anterior gonopod, lateral view. Fig. 295. Right posterior gonopod, anterior view. Fig. 296. Cyphopods, posterior view. Figs. 297–300. *C. inexpectata*. Fig. 297. Anterior gonopods, anterior view. Fig. 298. Left anterior gonopod, lateral view. Fig. 299. Right posterior gonopod, anterior view. Fig. 300. Cyphopods, posterior view. Fig. 301. *C. nantahala*, anterior gonopods, anterior view. Scale line = 0.75 mm for Figs. 297, 298; 0.45 mm for Fig. 294; 0.90 mm for posterior gonopods; 0.35 mm for cyphopods; 0.35 mm for Fig. 301.



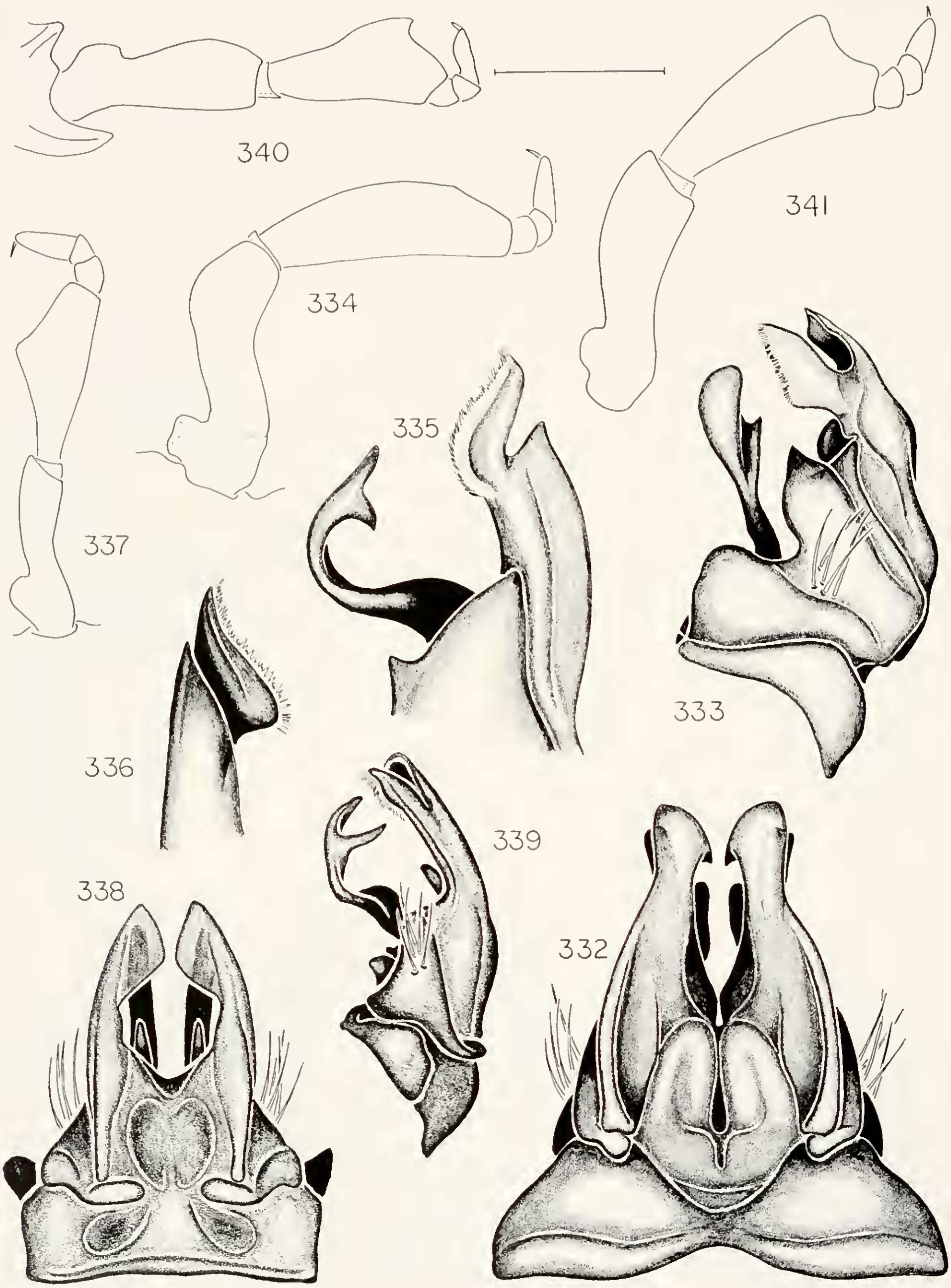
Figures 302–311. Anatomy of *Cleidogona* spp. Figs. 302–306. *C. nantahala*. Fig. 302. Left anterior gonopod, lateral view. Fig. 303. Right posterior gonopod, anterior view. Fig. 304. Right coxa 10, anterior view. Fig. 305. Process of sternum 12, lateral view. Fig. 306. Cyphopods, posterior view. Figs. 307–309. *C. lachesis*. Fig. 307. Anterior gonopods, anterior view. Fig. 308. Left anterior gonopod, lateral view. Fig. 309. Right posterior gonopod, anterior view. Figs. 310–311. *C. margarita*. Fig. 310. Anterior gonopods, anterior view. Fig. 311. Left anterior gonopod, lateral view. Scale line = 0.45 mm for anterior gonopods; 0.75 mm for posterior gonopods; 0.35 mm for Figs. 304–306.



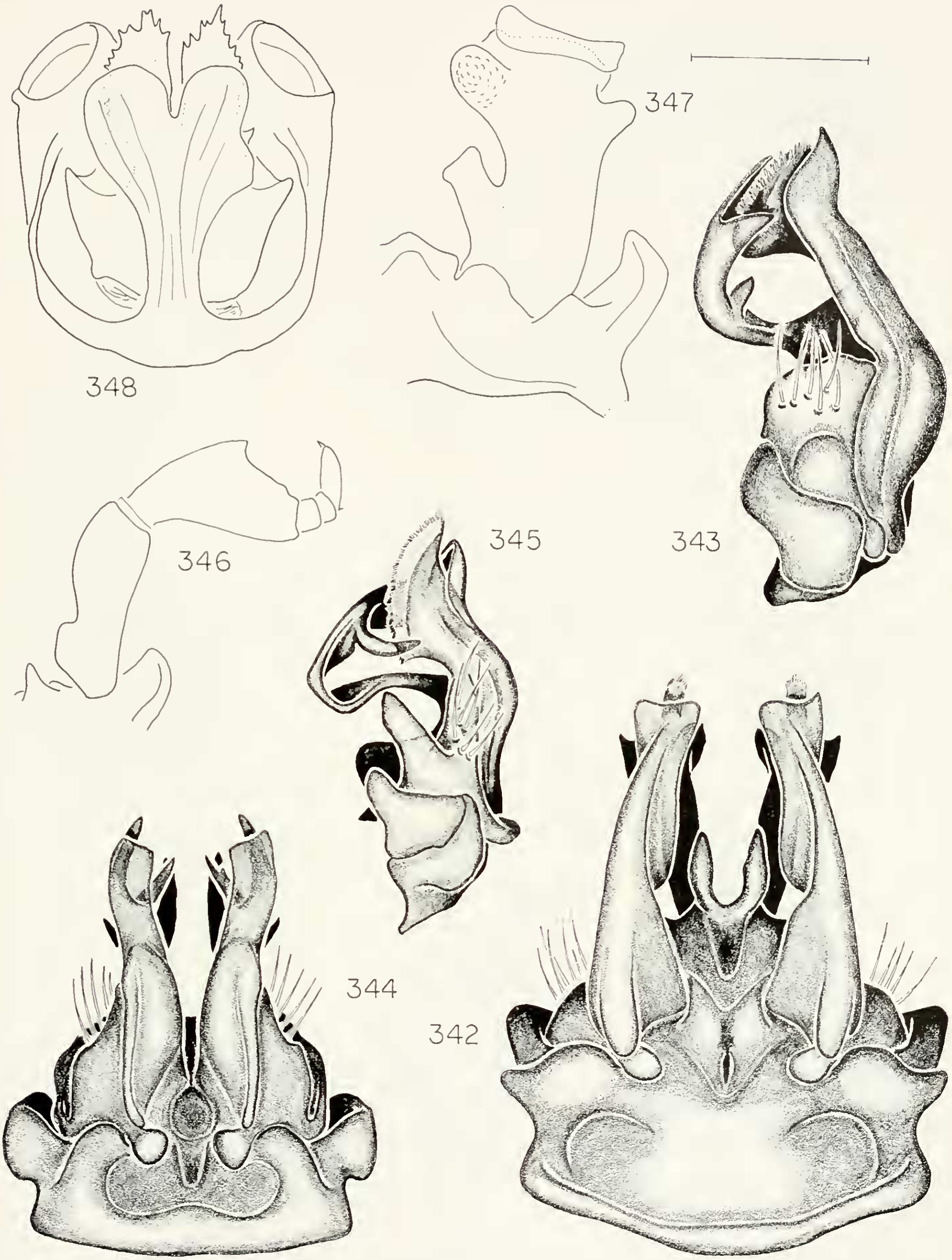
Figures 312–321. Anatomy of *Cleidogona* spp. Figs. 312–315. *C. margarita.* Fig. 312. Right posterior gonopod, anterior view. Fig. 313. Left coxa 11, posterior view. Fig. 314. Process of sternum 12, lateral view. Fig. 315. Cyphopods, posterior view. Figs 316–319. *C. jocassee.* Fig. 316. Anterior gonopods, anterior view. Fig. 317. Left anterior gonopod, lateral view. Fig. 318. Right posterior gonopod, anterior view. Fig. 319. Cyphopods, posterior view. Figs. 320–321. *C. hoffmani.* Fig. 320. Anterior gonopods, anterior view. Fig. 321. Left anterior gonopod, lateral view. Scale lines = 0.75 mm for Figs. 312, 318; 0.35 mm for Figs. 313, 314, 319; 0.25 mm for Figs. 315; 0.60 mm for Figs. 316, 317; 0.45 mm for Figs. 320, 321.



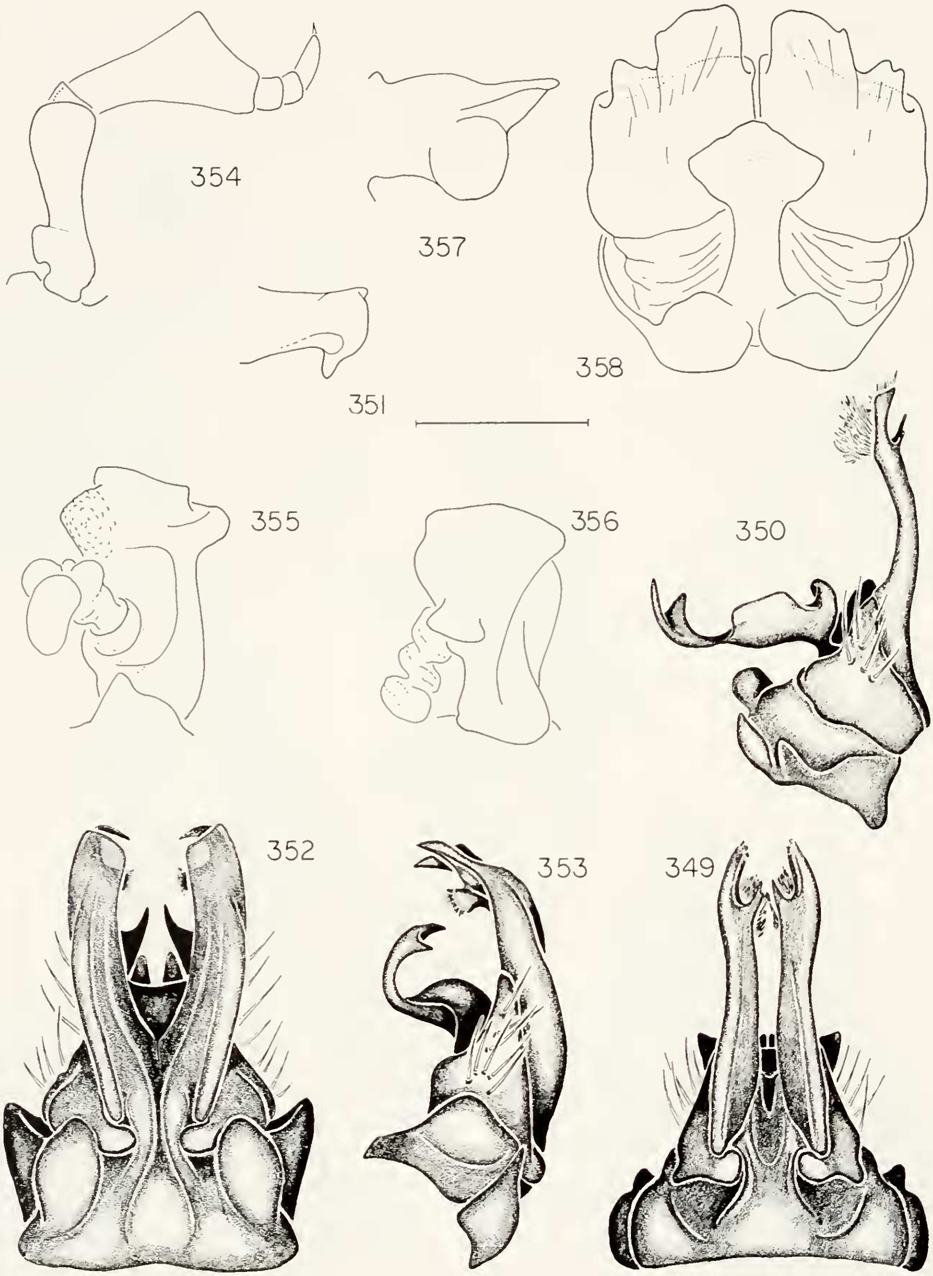
Figures 322–331. Anatomy of *Cleidogona* spp. Figs. 322–327. *C. hoffmani*. Figs. 322–323. Tips of anterior gonopod colpocoxites. Fig. 322. Specimen from Mt. Rogers, Va. Fig. 323. Specimen from Beartown Mt., Va. Fig. 324. Right posterior gonopod, anterior view. Fig. 325. Left coxa 11, posterior view. Fig. 326. Postgenital plate, posterior view. Fig. 327. Right cyphopods, lateral view. Figs. 328–331. *C. atropos*. Fig. 328. Apical part of anterior gonopod colpocoxites, anterior view. Fig. 329. Left anterior gonopod, lateral view. Fig. 330. Right posterior gonopod, anterior view. Fig. 331. Cyphopods, posterior view. Scale line = 0.25 mm for anterior gonopods; 0.75 mm for posterior gonopods; 0.35 mm for coxa and cyphopods.



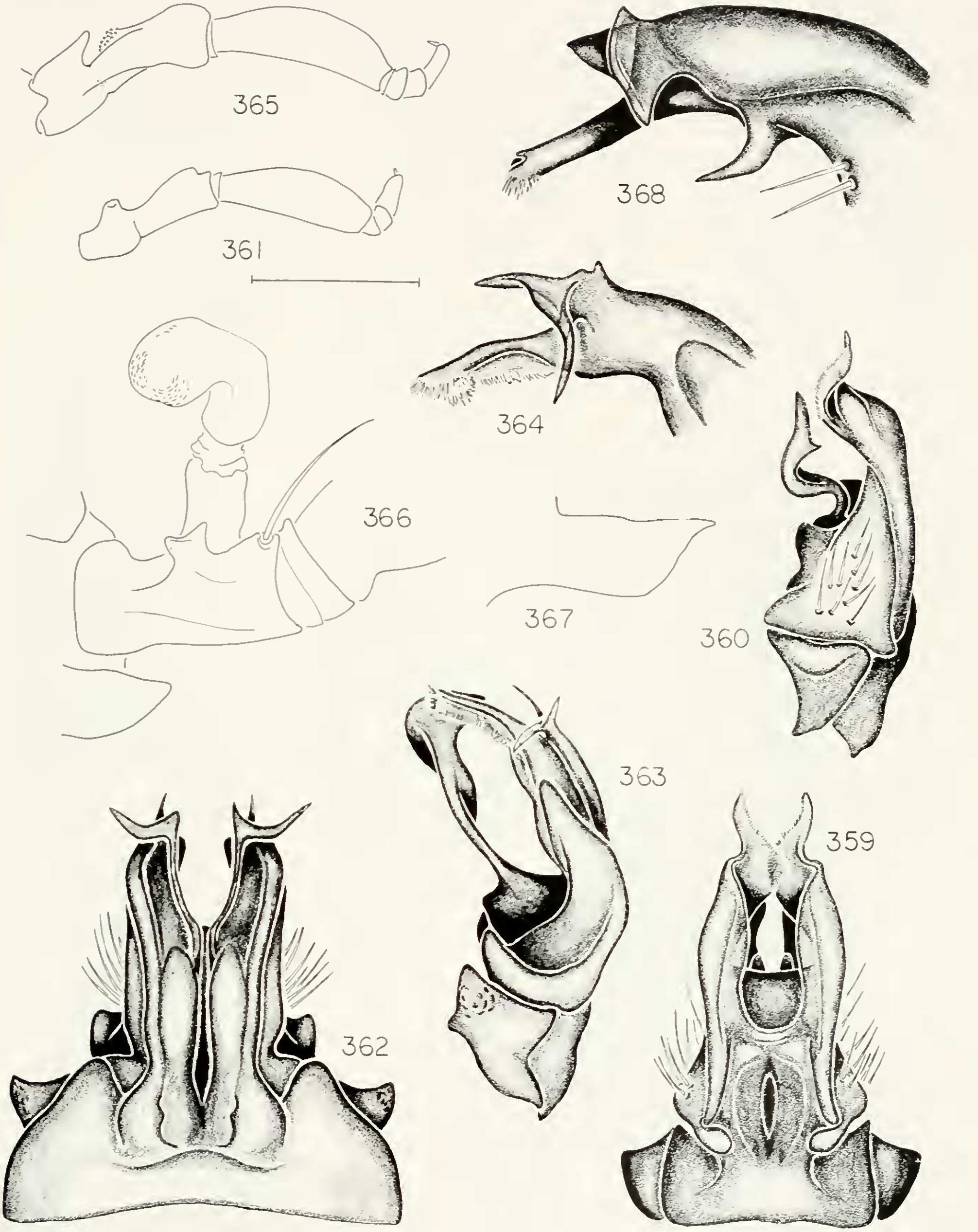
Figures 332–341. Anatomy of *Cleidogona* spp. Figs. 332–334. *C. tallapoosa*. Fig. 332. Anterior gonopods, anterior view. Fig. 333. Left anterior gonopod, lateral view. Fig. 334. Right posterior gonopod, anterior view. Figs. 335–337. *C. hadena*. Fig. 335. Left anterior gonopod, lateral view. Fig. 336. Left anterior gonopod colpocoxite tip, anterior view. Fig. 337. Right posterior gonopod, anterior view. Figs. 338–340. *C. caroliniana*. Fig. 338. Anterior gonopods, anterior view. Fig. 339. Left anterior gonopod, lateral view. Fig. 340. Right posterior gonopod, anterior view. Fig. 341. *C. fidelitor*, right posterior gonopod, anterior view. Scale line = 0.45 mm for Figs. 332, 333, 338, 339; 0.25 mm for Figs. 335, 336; 0.75 mm for Figs. 337, 340; 0.35 mm for Fig. 341.



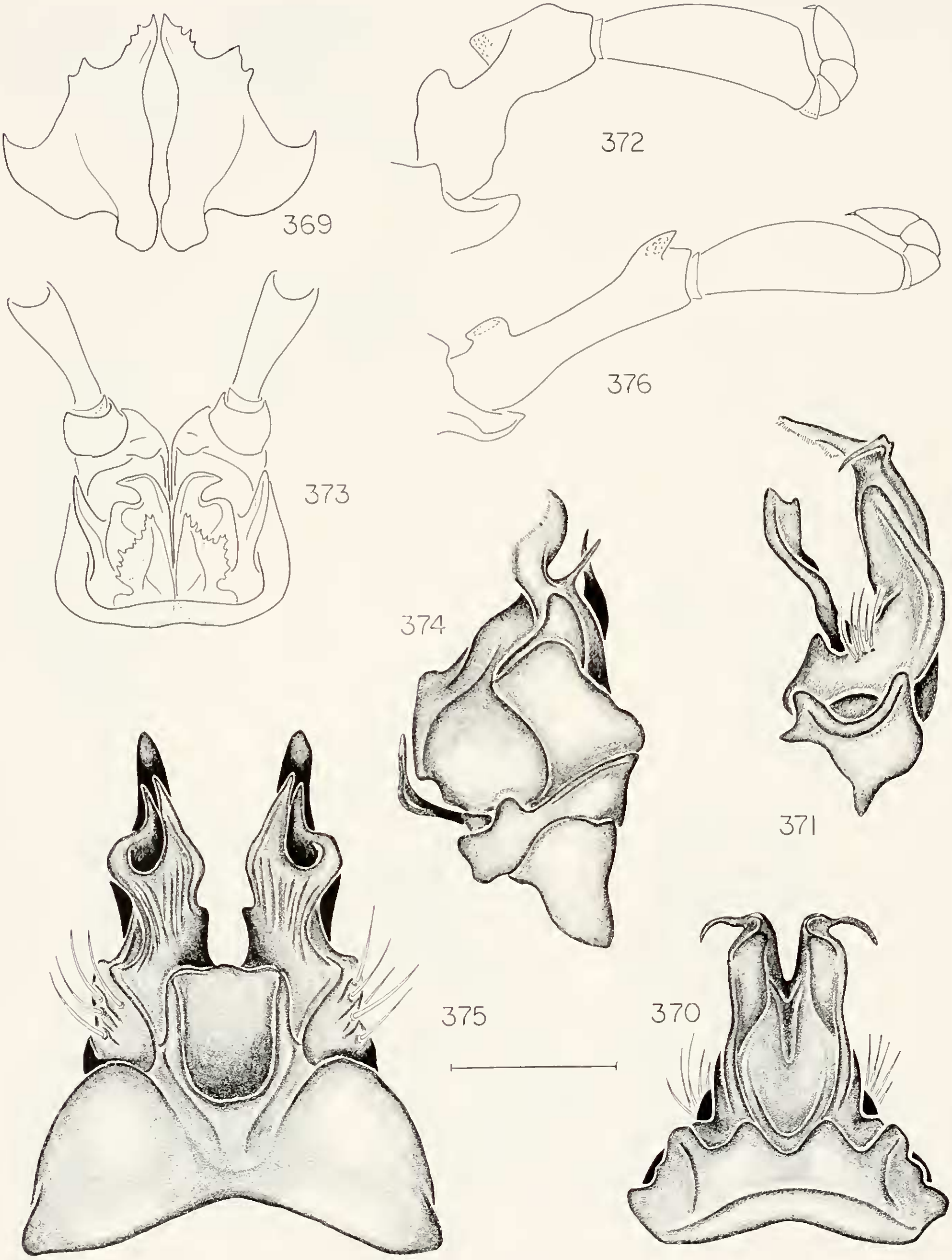
Figures 342–348. Anatomy of *Cleidogona* spp. Figs. 342–343. *C. fidelitor*. Fig. 342. Anterior gonopods, anterior view. Fig. 343. Left anterior gonopod, lateral view. Figs. 344–348. *C. steno*. Fig. 344. Anterior gonopods, anterior view. Fig. 345. Left anterior gonopod, lateral view. Fig. 346. Right posterior gonopod, anterior view. Fig. 347. Right coxa 10, anterior view. Fig. 348. Cyphopods, posterior view. Scale line = 0.45 mm for Figs. 344–346; 0.25 mm for Figs. 342, 343, 347, 348.



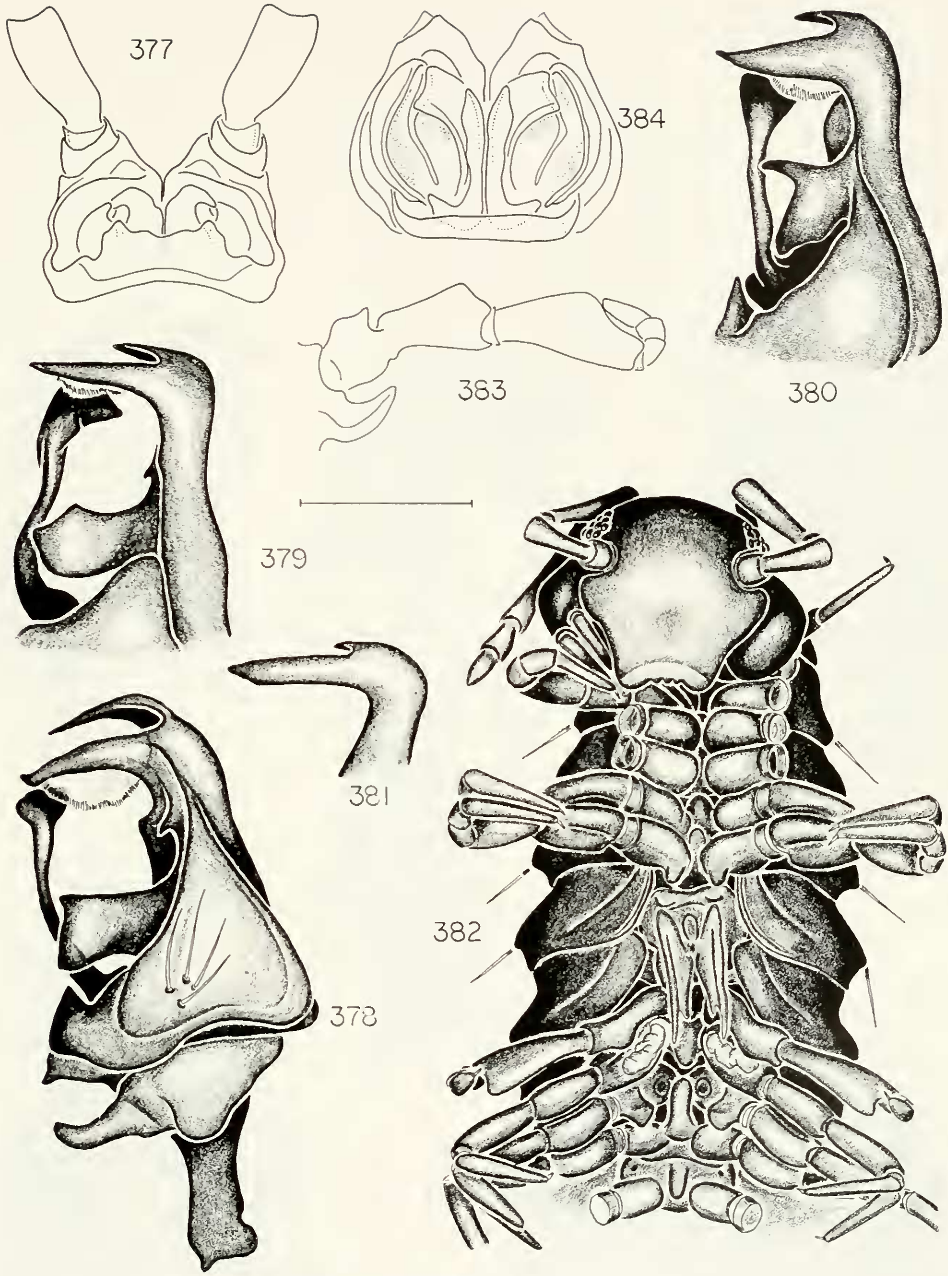
Figures 349–358. Anatomy of *Cleidogona* spp. Figs. 349–351. *C. alata.* Fig. 349. Anterior gonopods, anterior view. Fig. 350. Left anterior gonopod, lateral view. Fig. 351. Process of sternum 12, lateral view. Figs. 352–358. *C. georgia.* Fig. 352. Anterior gonopods, anterior view. Fig. 353. Left anterior gonopod, lateral view. Fig. 354. Right posterior gonopod, anterior view. Fig. 355. Right coxa 10, anterior view. Fig. 356. Left coxa 11, posterior view. Fig. 357. Process of sternum 12, lateral view. Fig. 358. Cyphopods, posterior view. Scale line = 0.45 mm for anterior gonopods, 0.35 mm for Figs. 355, 356; 0.25 mm for Figs. 351, 358; 0.75 mm for Fig. 354.



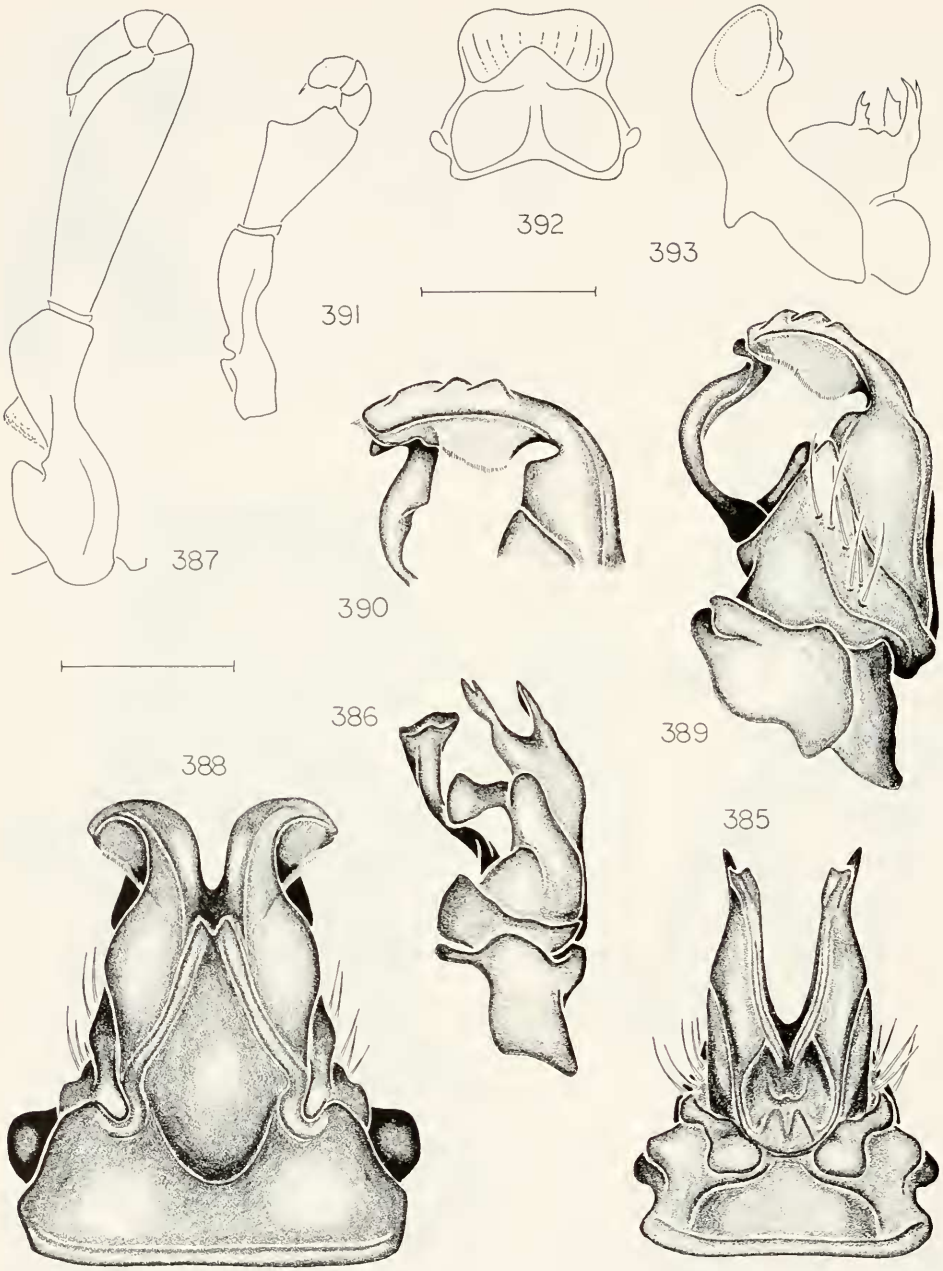
Figures 359–368. Anatomy of *Cleidogona* spp. Figs. 359–361. *C. wrayi*. Fig. 359. Anterior gonopods, anterior view. Fig. 360. Left anterior gonopod, lateral view. Fig. 361. Right posterior gonopod, anterior view. Figs. 362–367. *C. grenada*. Fig. 362. Anterior gonopods, anterior view. Fig. 363. Left anterior gonopod, lateral view. Fig. 364. Tip of left anterior gonopod colpocoxite, lateral view. Fig. 365. Right posterior gonopod, anterior view. Fig. 366. Left coxa 11, posterior view. Fig. 367. Process of sternum 12, lateral view. Fig. 368. *C. mississippiana*, tip of colpocoxite of left anterior gonopod, lateral view. Scale line = 0.45 mm for Figs. 359, 360, 362, 363; 0.25 mm for Figs. 364, 366–368; 0.75 mm for posterior gonopods.



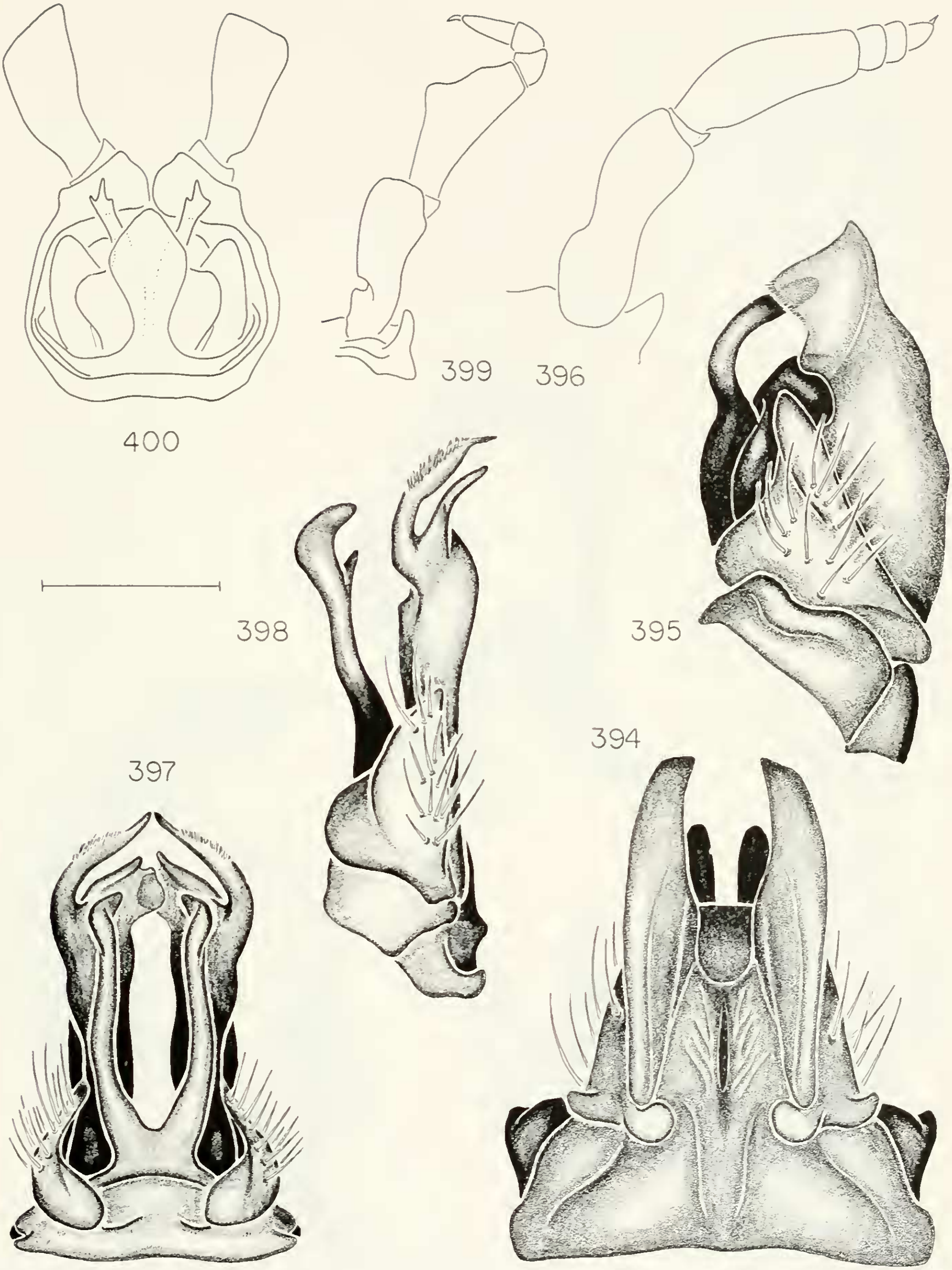
Figures 369–376. Anatomy of *Cleidogona* spp. Fig. 369. *C. grenada*, postgenital plate, posterior view. Figs. 370–373. *C. sublettei*. Fig. 370. Anterior gonopods, anterior view. Fig. 371. Left anterior gonopod, lateral view. Fig. 372. Right posterior gonopod, anterior view. Fig. 373. Cyphopods, posterior view. Figs. 374–376. *C. celerita*. Fig. 374. Left anterior gonopod, lateral view. Fig. 375. Anterior gonopods, anterior view. Fig. 376. Right posterior gonopod, anterior view. Scale line = 0.60 mm for Figs. 370, 371; 0.75 mm for Figs. 373–375; 0.90 mm for Figs. 372, 376; 0.25 mm for Fig. 369.



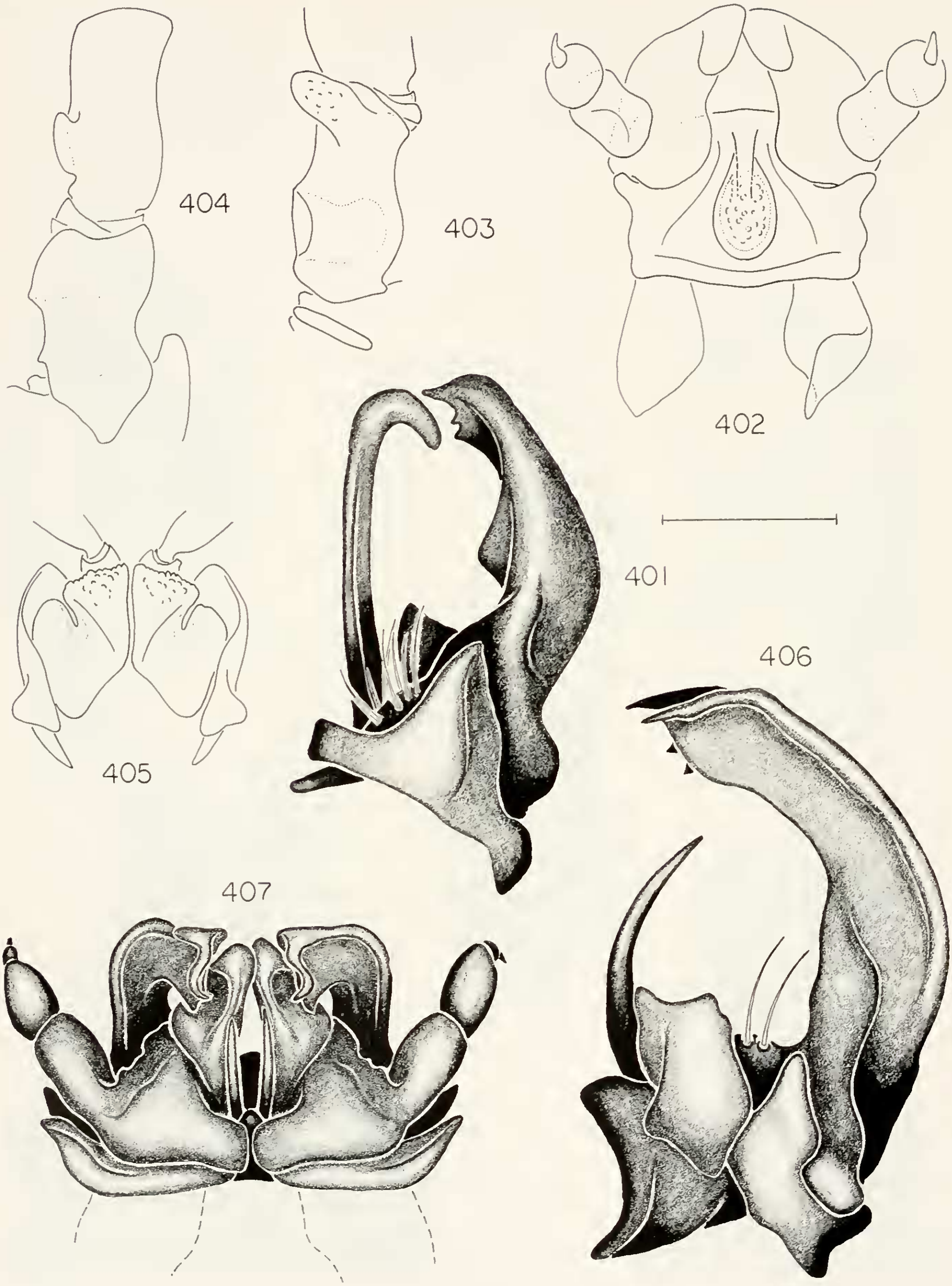
Figures 377–384. Anatomy of *Cleidogona* spp. Fig. 377. *C. celerita*, cyphopods, posterior view. Figs. 378–384. *C. caesioannulata*. Fig. 378. Left anterior gonopod, lateral view, specimen from Wooster, Ohio. Figs. 379–381. Tips of left anterior gonopod colpocoxites. Fig. 379. Specimen from Peaks of Otter, Va. Fig. 380. Specimen from Mt. Mitchell, N. Car. Fig. 381. Specimen from Clifton Forge, Va. Fig. 382. Anterior end of body of male, ventral view. Fig. 383. Right posterior gonopod, anterior view. Fig. 384. Cyphopods, posterior view (specimen from Wooster, Ohio, compared with female holotype). Scale line = 0.50 mm for Figs. 378–381; 0.90 mm for Fig. 382; 1.00 mm for Fig. 383; 0.75 mm for Figs. 377, 384.



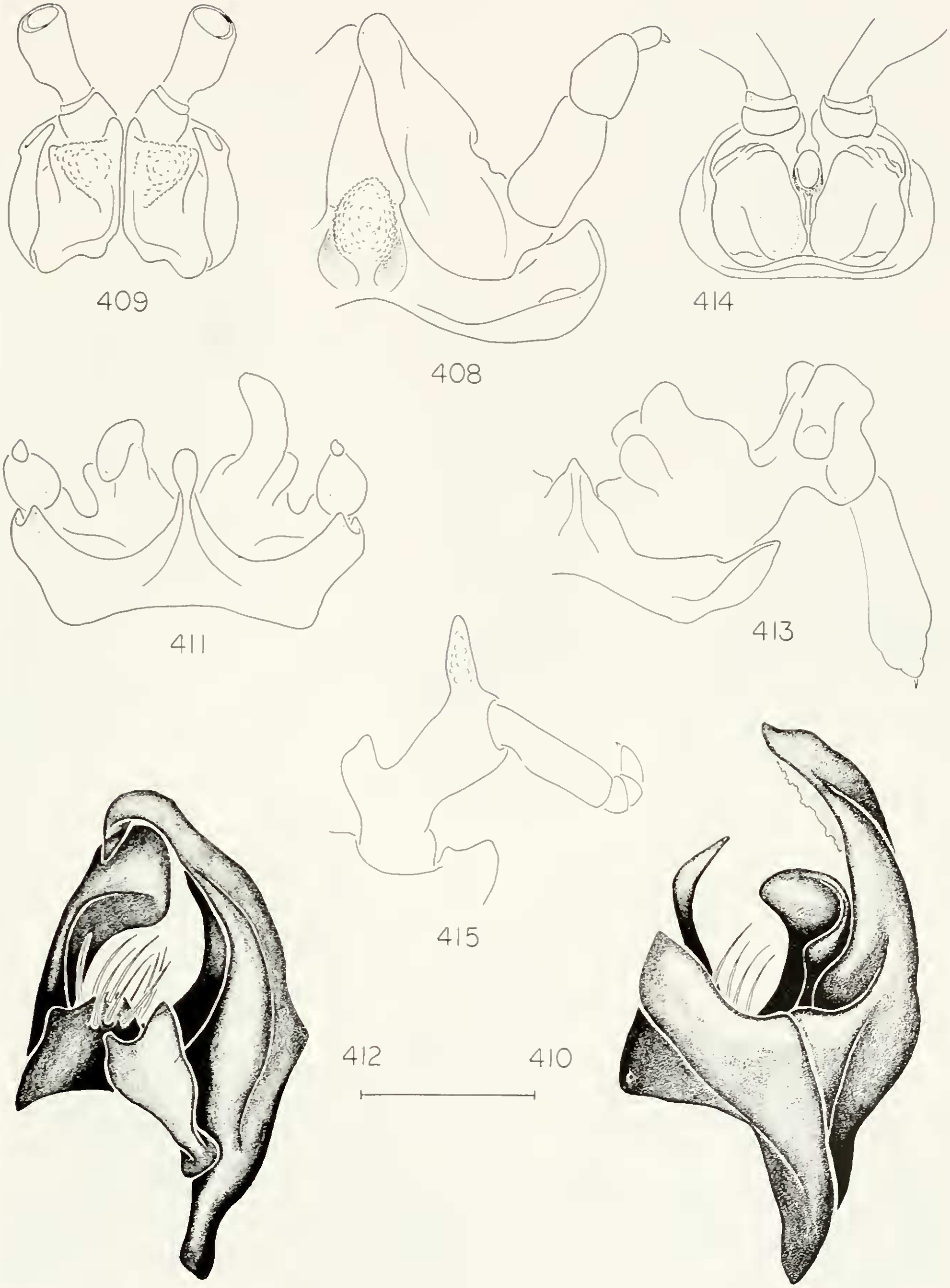
Figures 385–393. Anatomy of *Cleidogona* spp. Figs. 385–387. *C. laminata*. Fig. 385. Anterior gonopods, anterior view. Fig. 386. Left anterior gonopod, lateral view. Fig. 387. Right posterior gonopod, anterior view. Figs. 388–393. *C. unita*. Fig. 388. Anterior gonopods, anterior view. Fig. 389. Left anterior gonopod, lateral view. Fig. 390. Tip of colpocoxite of left anterior gonopod of specimen from Mammoth Cave National Park, Ky., lateral view. Fig. 391. Right posterior gonopod, anterior view. Fig. 392. Postgenital plate, posterior view. Fig. 393. Right cyphopods and coxa 2, lateral view. Scale lines = 0.35 mm for Figs. 388–390; 0.60 mm for Figs. 385–387; 0.75 mm for Fig. 381; 0.35 mm for Figs. 392, 393.



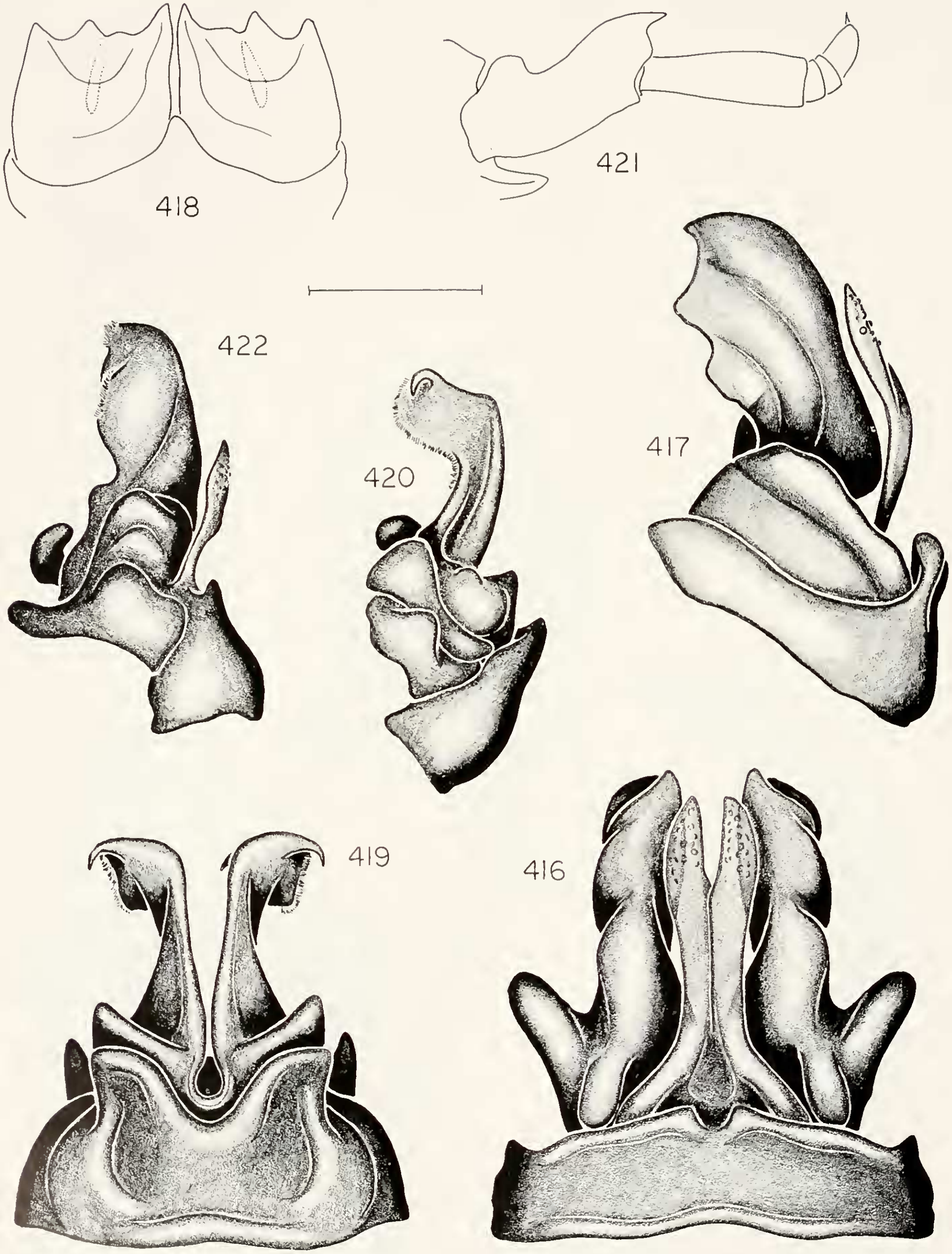
Figures 394–400. Anatomy of *Cleidogona* spp. Figs. 394–396. *C. accretis*. Fig. 394. Anterior gonopods, anterior view. Fig. 395. Left anterior gonopod, lateral view. Fig. 396. Right posterior gonopod, anterior view. Figs. 397–400. *C. fustis*. Fig. 397. Anterior gonopods, posterior view. Fig. 398. Left anterior gonopod, lateral view. Fig. 399. Right posterior gonopod, anterior view. Fig. 400. Cyphopods, anterior view. Scale line = 0.50 mm for Figs. 397, 398, 400; 0.25 mm for Figs. 394–395; 0.35 mm for Fig. 396; 0.90 mm for Fig. 399.



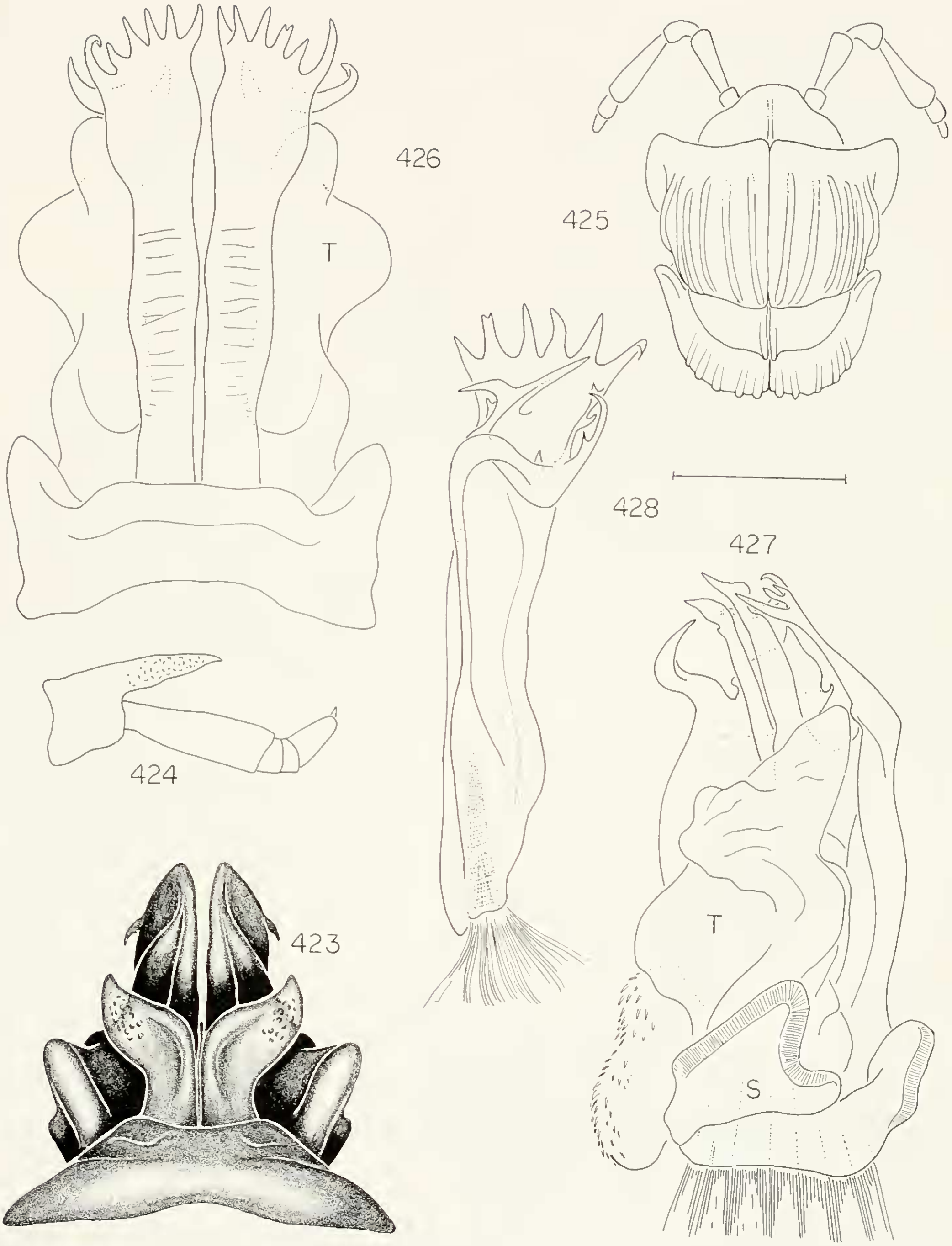
Figures 401–407. Anatomy of *Tiganogona* spp. Figs. 401–405. *T. brownae*. Fig. 401. Left anterior gonopod, anterior view. Fig. 402. Posterior gonopods, anterior view. Fig. 403. Right coxa 10, anterior view. Fig. 404. Right coxa, trochanter, and prefemur 11, anterior view. Fig. 405. Cyphopods, posterior view. Figs. 406–407. *T. moesta*. Fig. 406. Left anterior gonopod, anterior view. Fig. 407. Anterior and posterior gonopods *in situ*, posterior view. Scale line = 0.75 mm for Fig. 405; 0.35 mm for Figs. 401–404, 406, 407.



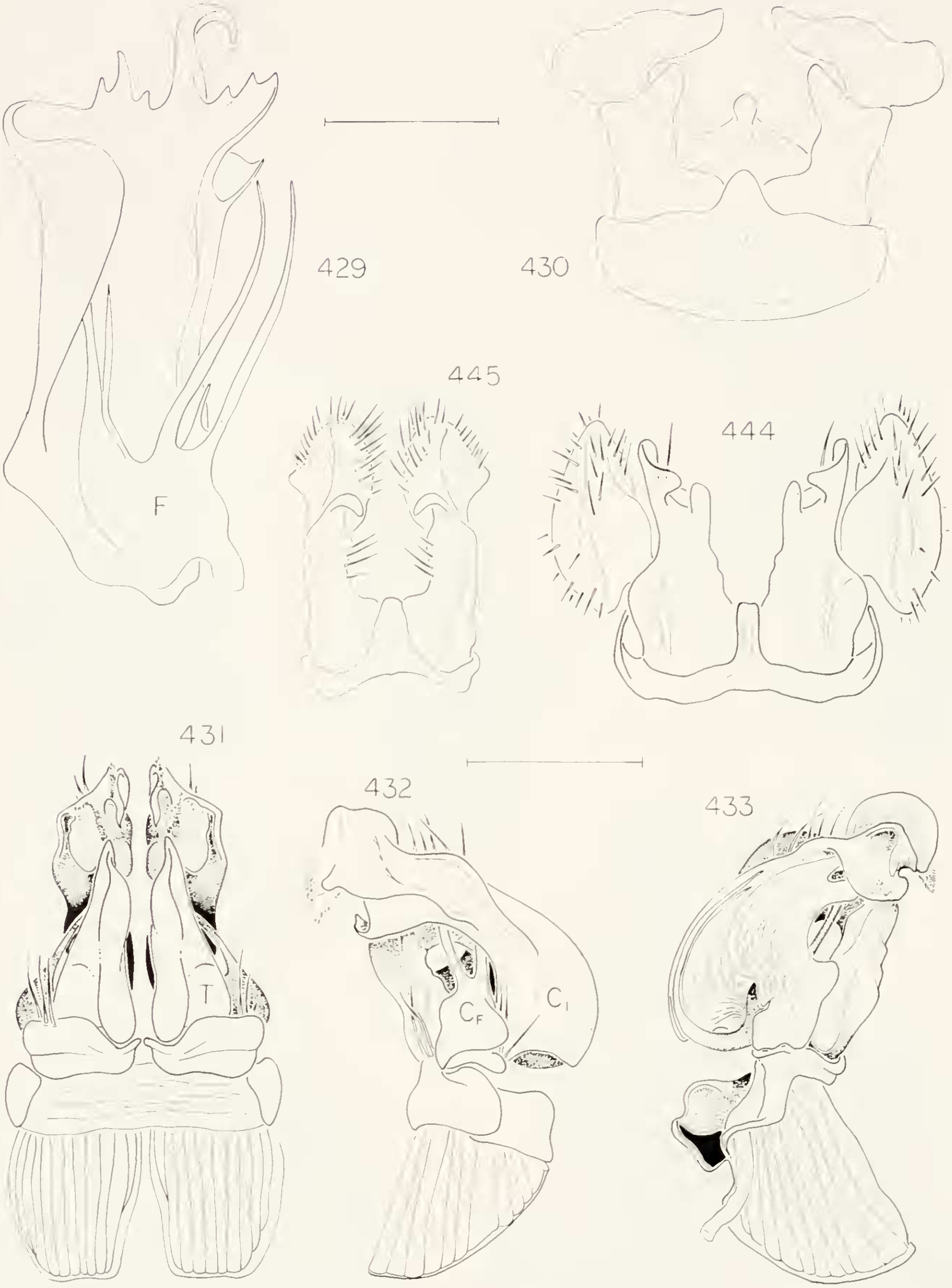
Figures 408–415. Anatomy of *Tiganogona* and *Dybasia* spp. Figs. 408–409. *Tiganogona moesta*. Fig. 408. Right posterior gonopod, anterior view. Fig. 409. Cyphopods, posterior view. Figs. 410–411. *T. alia*. Fig. 410. Left anterior gonopod, lateral view. Fig. 411. Posterior gonopods, anterior view. Figs. 412–414. *T. glebosa*. Fig. 412. Left anterior gonopod, lateral view. Fig. 413. Right posterior gonopod, anterior view. Fig. 414. Cyphopods, posterior view. Fig. 415. *Dybasia humerosa*, right posterior gonopod, anterior view. Scale line = 0.35 mm for anterior and posterior gonopods, 0.75 mm for cyphopods.



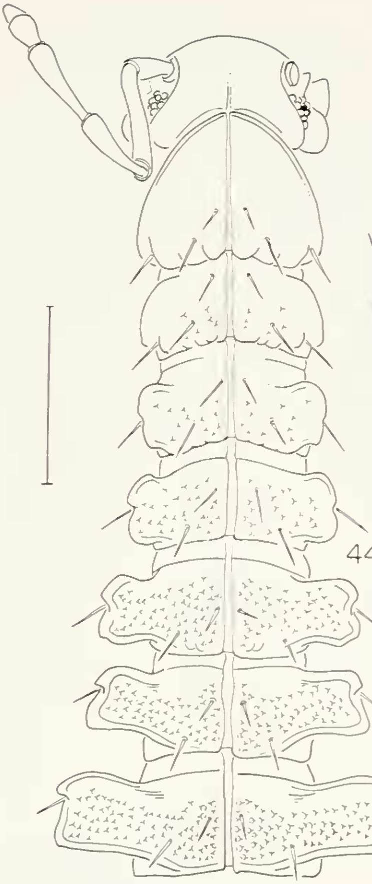
Figures 416–422. Anatomy of *Dybasia* spp. Figs. 416–418. *D. humerosa*. Fig. 416. Anterior gonopods, anterior view. Fig. 417. Left anterior gonopod, lateral view. Fig. 418. Cyphopods, posterior view. Figs. 419–421. *D. divergens*. Fig. 419. Anterior gonopods, anterior view. Fig. 420. Left anterior gonopod, lateral view. Fig. 421. Right posterior gonopod, anterior view. Fig. 422. *D. chiriquia*, left anterior gonopod, lateral view. Scale lines = 0.35 mm for Fig. 421, 0.25 mm for Figs. 416–420, 422.



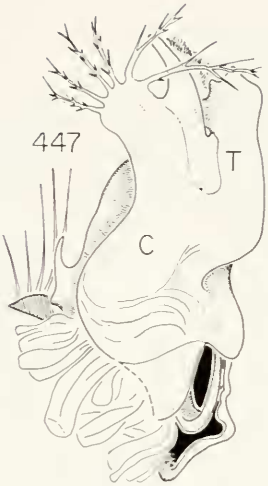
Figures 423–428. Anatomy of *Dybasia* and *Striaria* spp. Figs. 423–424. *Dybasia chiriquia.* Fig. 423. Anterior gonopods, anterior view. Fig. 424. Right posterior gonopod, anterior view. Figs. 425–428. *Striaria* sp. Fig. 425. Anterior end of body, dorsal view. Fig. 426. Anterior gonopods, anterior view. Fig. 427. Left anterior gonopod, lateral view. Fig. 428. Left anterior gonopod, anterior colpocoxite, posterior view. Scale line = 0.25 mm for Figs. 423, 424; 0.90 mm for Fig. 425; 0.10 mm for Figs. 426–428.



Figures 429–445. Anatomy of *Striaria* sp., *Caseya heteropus*, and *Urochordeuma porona*. Figs. 429–430. *Striaria* sp. Fig. 429. Posterior colpocoxite of left anterior gonopod, mesal view. Fig. 430. Posterior gonopods, anterior view. Figs. 431–444. *Caseya heteropus*. Fig. 431. Anterior gonopods, posterior view. Fig. 432. Left anterior gonopod, lateral view. Fig. 433. Left anterior gonopod, mesal view. Fig. 444. Posterior gonopods, posterior view. Fig. 445. *Urochordeuma porona*, posterior gonopods, posterior view. Scale lines = 0.09 mm for Fig. 429; 0.75 mm for Figs. 431–444; 0.60 mm for Fig. 445; 0.35 mm for Fig. 430.

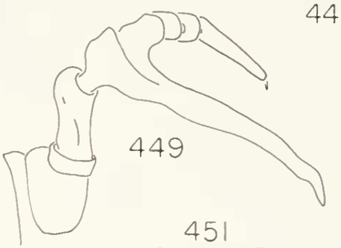


446

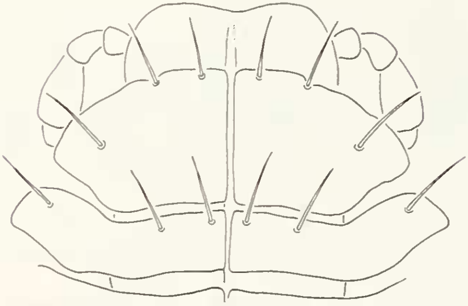


447

448

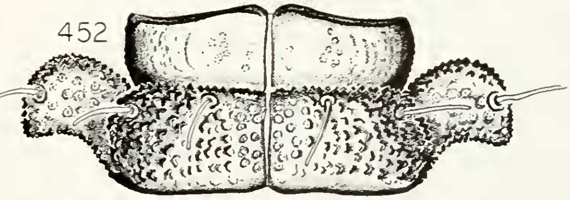


449



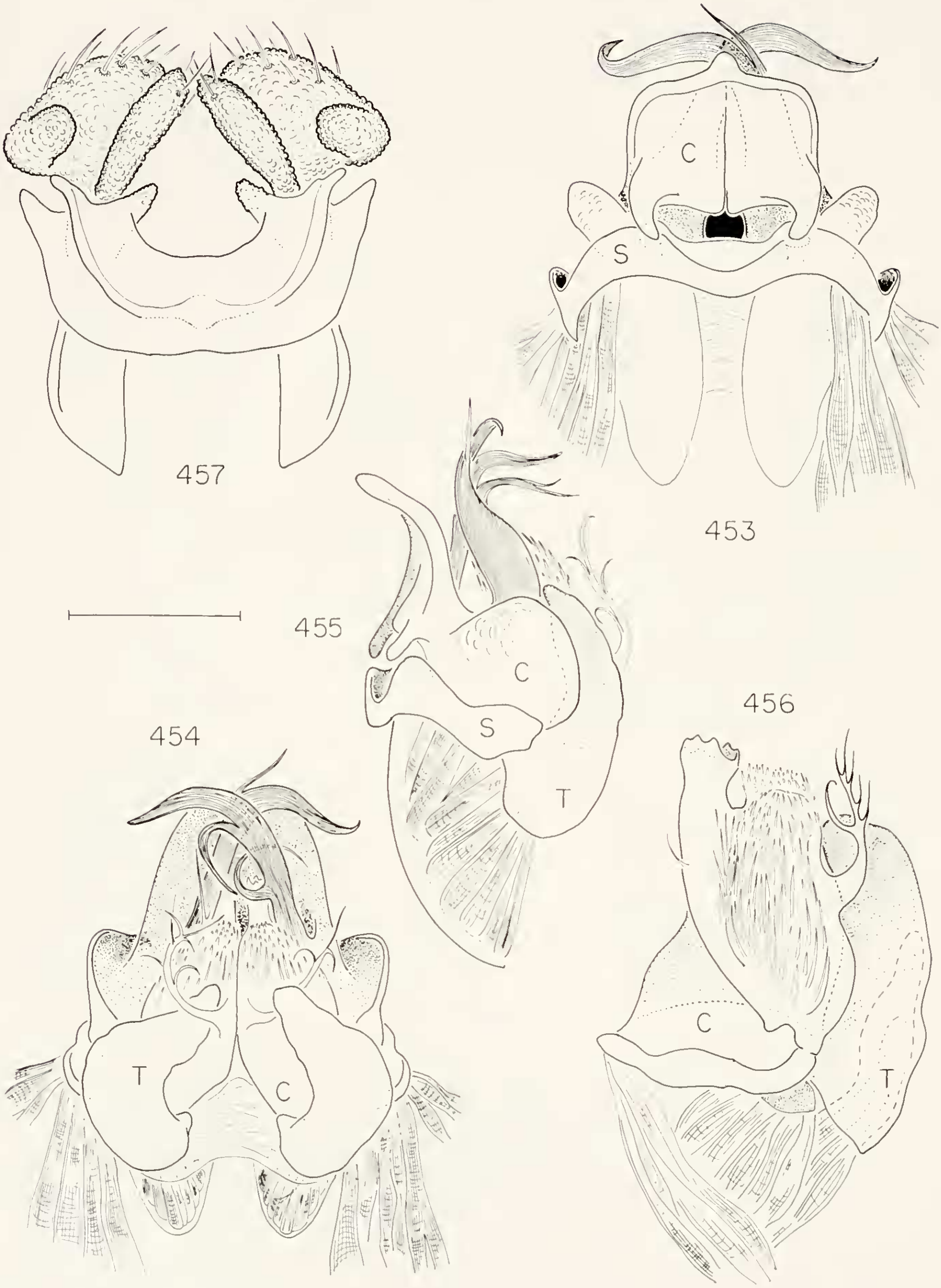
451

450



452

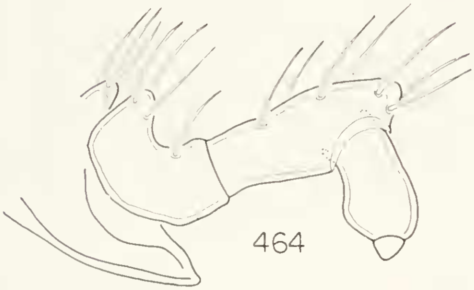
Figures 446–452. Anatomy of *Urochordeuma porona* and *Rhiscosomides acovescor*. Figs. 446–450. *Urochordeuma porona*. Fig. 446. Anterior end of body, dorsal view. Fig. 447. Left anterior gonopod, mesal view. Fig. 448. Left anterior gonopod, lateral view. Fig. 449. Right leg 1, posterior view. Fig. 450. Right leg 3, anterior view. Figs. 451–452. *Rhiscosomides acovescor*. Fig. 451. Anterior end of body, dorsal view, tergal sculpture omitted. Fig. 452. Segment 12, dorsal view. Scale line = 0.90 mm for Fig. 446; 0.60 mm for Figs. 447, 448; 0.75 mm for Figs. 449, 450; 0.45 mm for Figs. 451, 452.



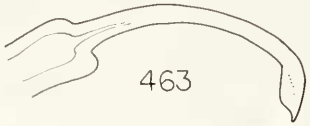
Figures 453–457. Anatomy of *Rhiscosomides acovescor*. Fig. 453. Anterior gonopods, anterior view. Fig. 454. Anterior gonopods, posterior view. Fig. 455. Anterior gonopods, lateral view. Fig. 456. Left posterior colpocoxite and telopodite of anterior gonopods, mesal view. Fig. 457. Posterior gonopods, posterior view. Scale line = 0.40 mm for Figs. 453–455; 0.20 mm for Figs. 456; 0.25 mm for Figs. 457.

458

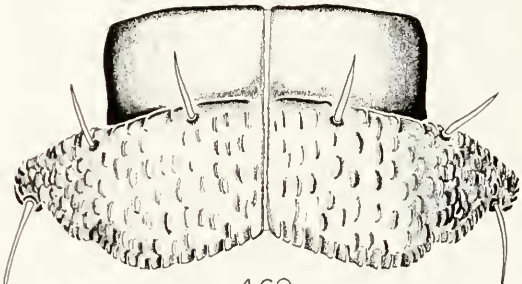
462



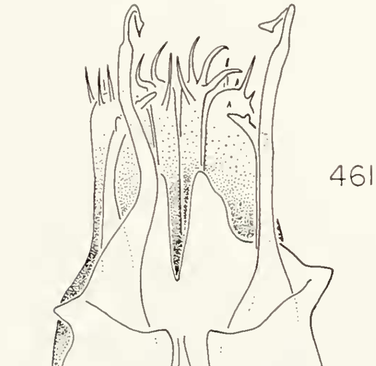
464



463

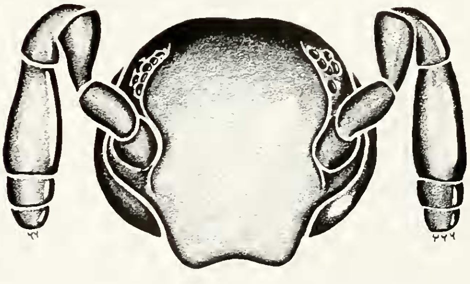


460

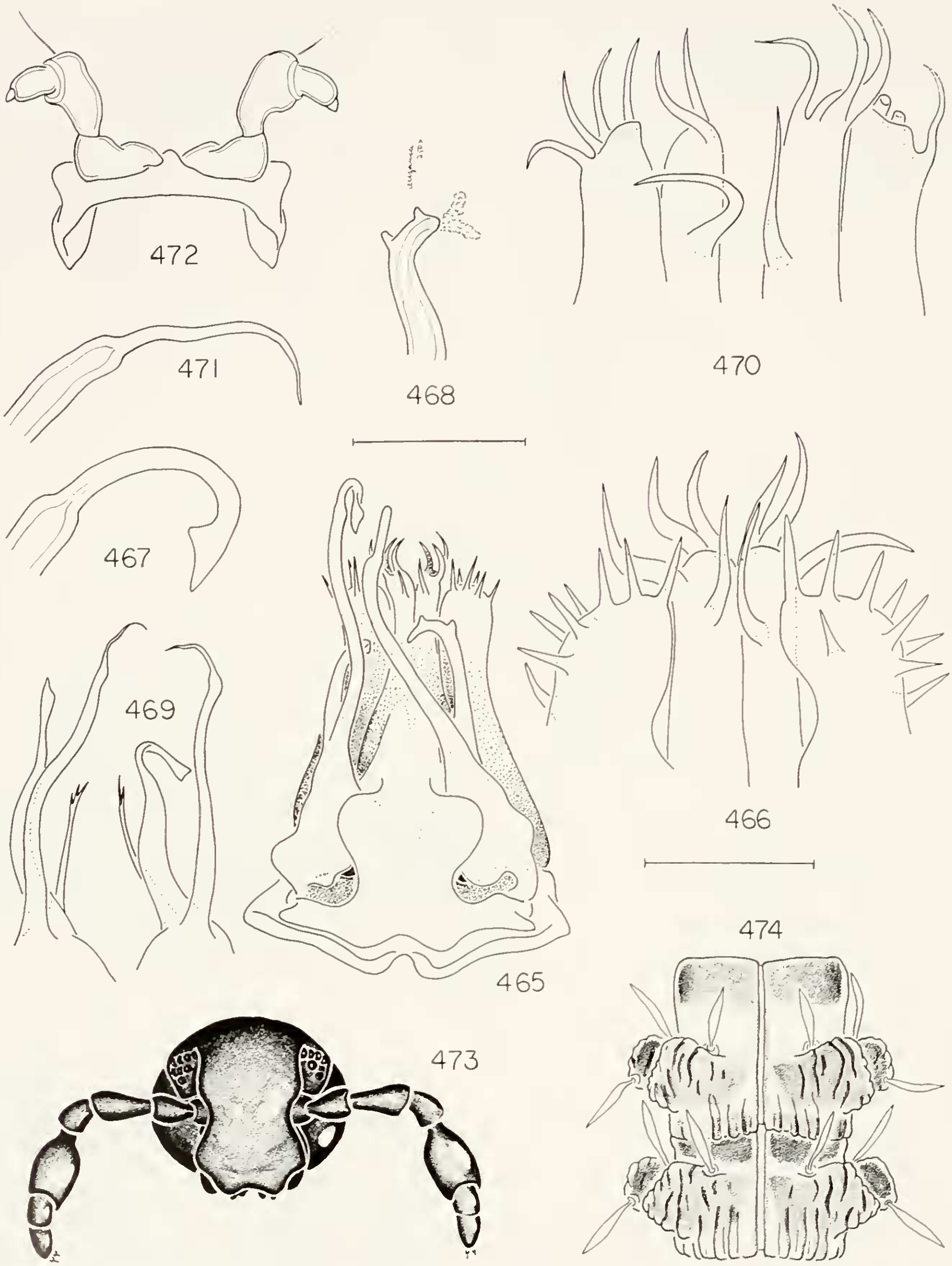


461

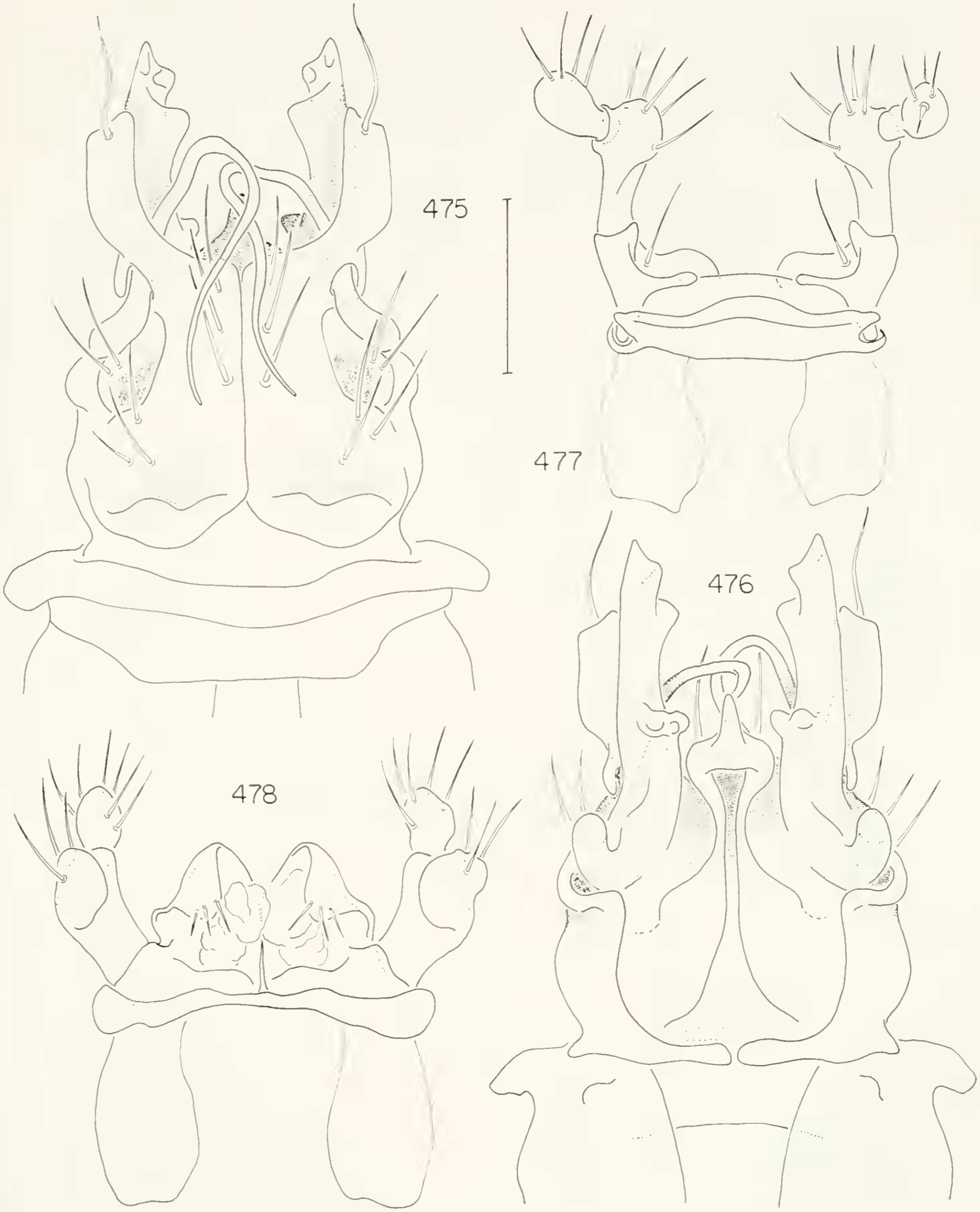
459



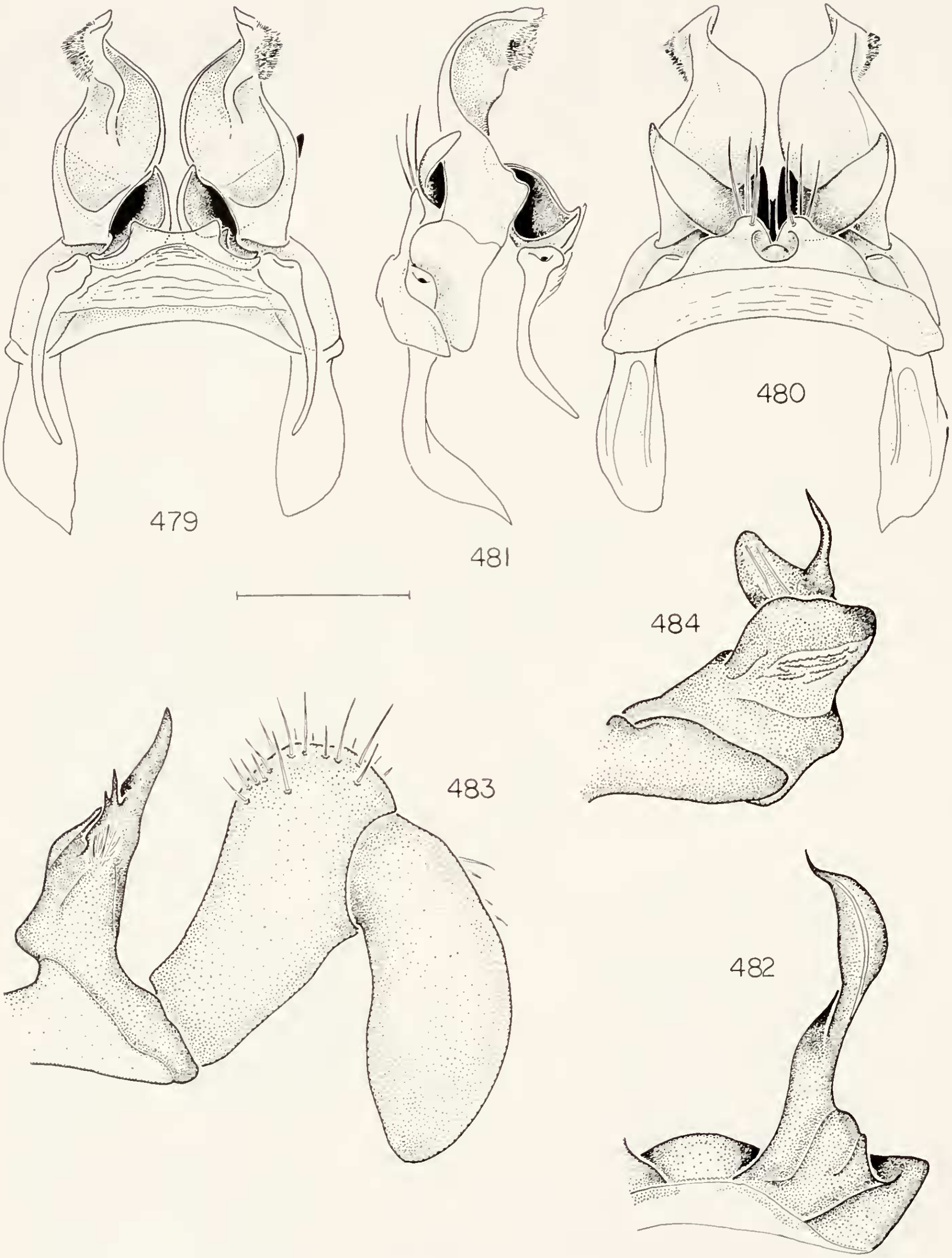
Figures 458–464. Anatomy of *Rhiscosomides acovescor* and *Tingupa utahensis*. Fig. 458. *Rhiscosomides acovescor*, posterior gonopods, anterior view. Figs. 459–463. *Tingupa utahensis*. Fig. 459. Head, anterior view. Fig. 460. Segment 12, dorsal view. Fig. 461. Anterior gonopods, posterior view. Fig. 462. Tips of anterior gonopod coxal processes, posterior view. Fig. 463. Tip of longest telopodite process of anterior gonopod, lateral view. Fig. 464. Right posterior gonopod, anterior view. Scale line = 0.25 mm for Figs. 458, 461, 464; 0.35 mm for Figs. 459, 460; 0.05 mm for Figs. 462, 463.



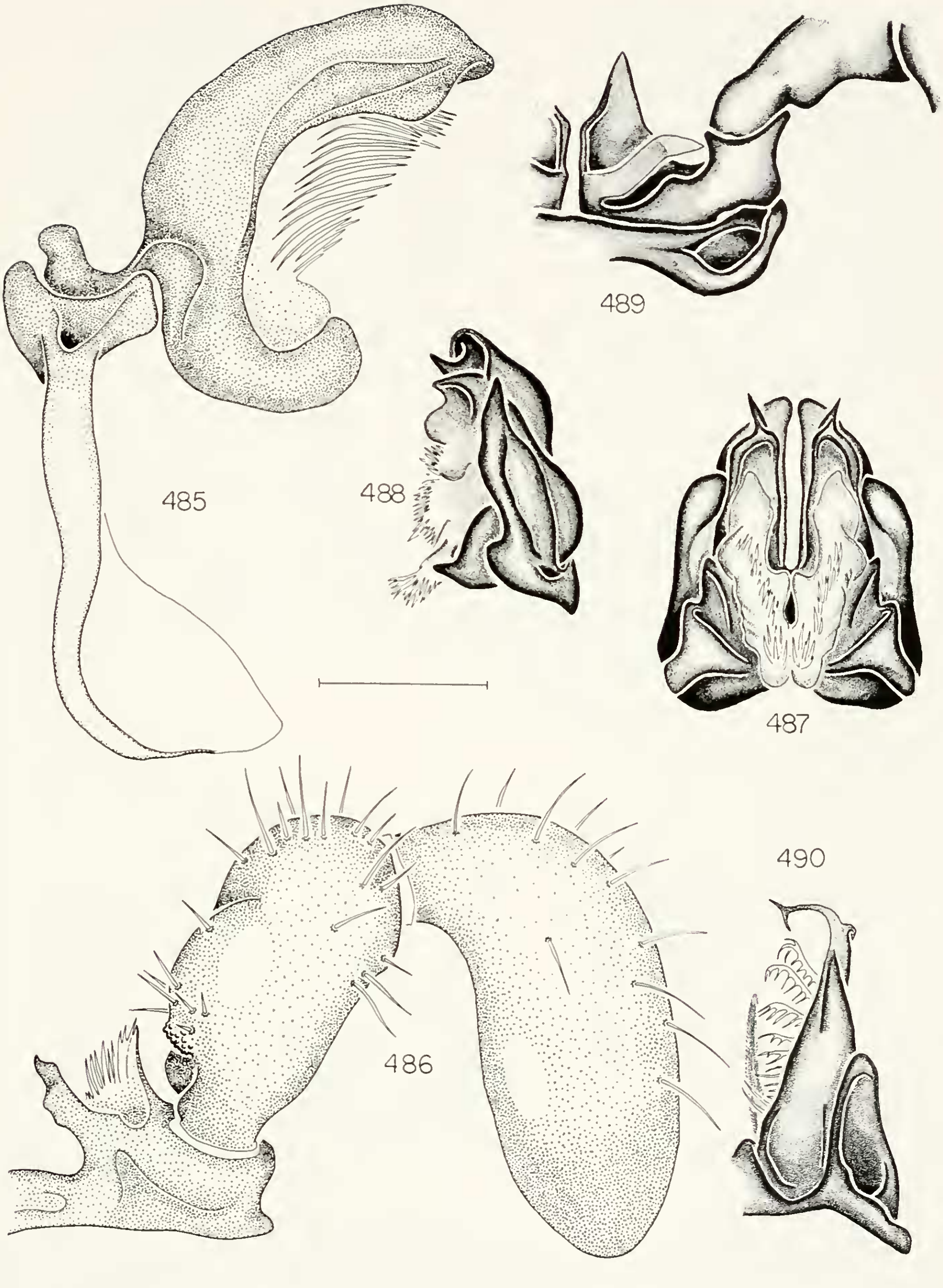
Figures 465–474. Anatomy of *Tingupa* spp. and *Branneria carinata*. Figs. 465–468. *Tingupa arizonica*. Fig. 465. Anterior gonapods, posterior view. Fig. 466. Tips of anteriar gonapad coxal pracesses, posteriar view. Fig. 467. Tip of longest telapadite process of anterior gonapod, lateral view. Fig. 468. Tip of shorter anterior gonopod telopodite process, lateral view. Figs. 469–472. *T. pallida*. Fig. 469. Telopodites of anterior gonopods, posterior view. Fig. 470. Tips of anterior gonapod coxal processes, pasteriar view. Fig. 471. Tip of longest anterior gonopod telopodite process, lateral view. Fig. 472. Posteriar gonapads, anterior view. Figs. 473–474. *Branneria carinata*. Fig. 473. Head, anterior view. Fig. 474. Segments 12, 13, darsal view. Scale line = 0.25 mm for Figs. 465, 469; 0.35 mm for Figs. 473, 474; 0.05 mm for Figs. 466–468, 470, 471; 0.50 mm for Fig. 472.



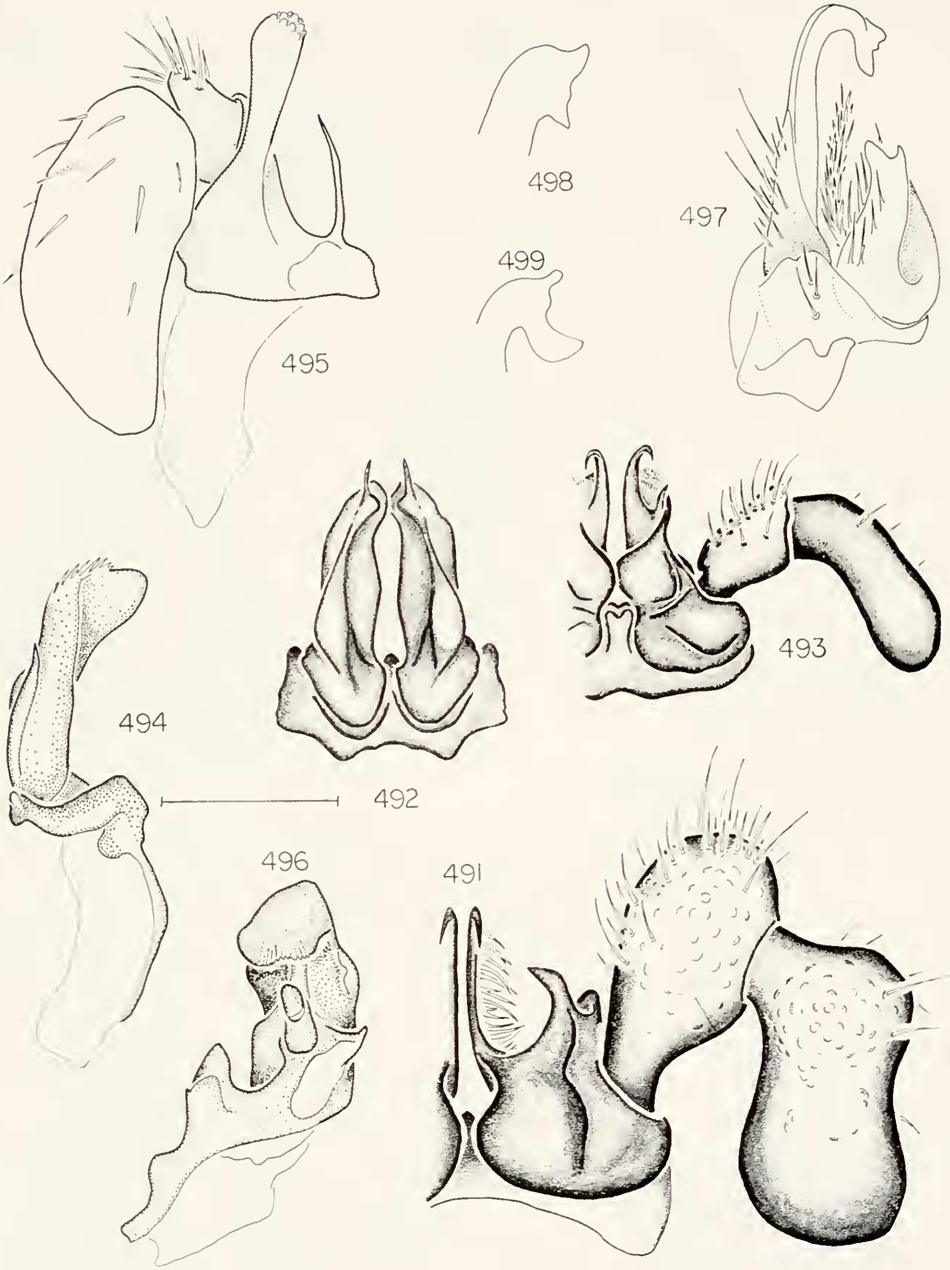
Figures 475–478. Anatomy of *Branneria carinata*. Fig. 475. Anterior gonopods, anterior view. Fig. 476. Anterior gonopods, posterior view. Fig. 477. Posterior gonopods, anterior view. Fig. 478. Legpair 10, anterior view. Scale line = 0.05 mm for Figs. 475, 476; 0.09 mm for Figs. 477, 478.



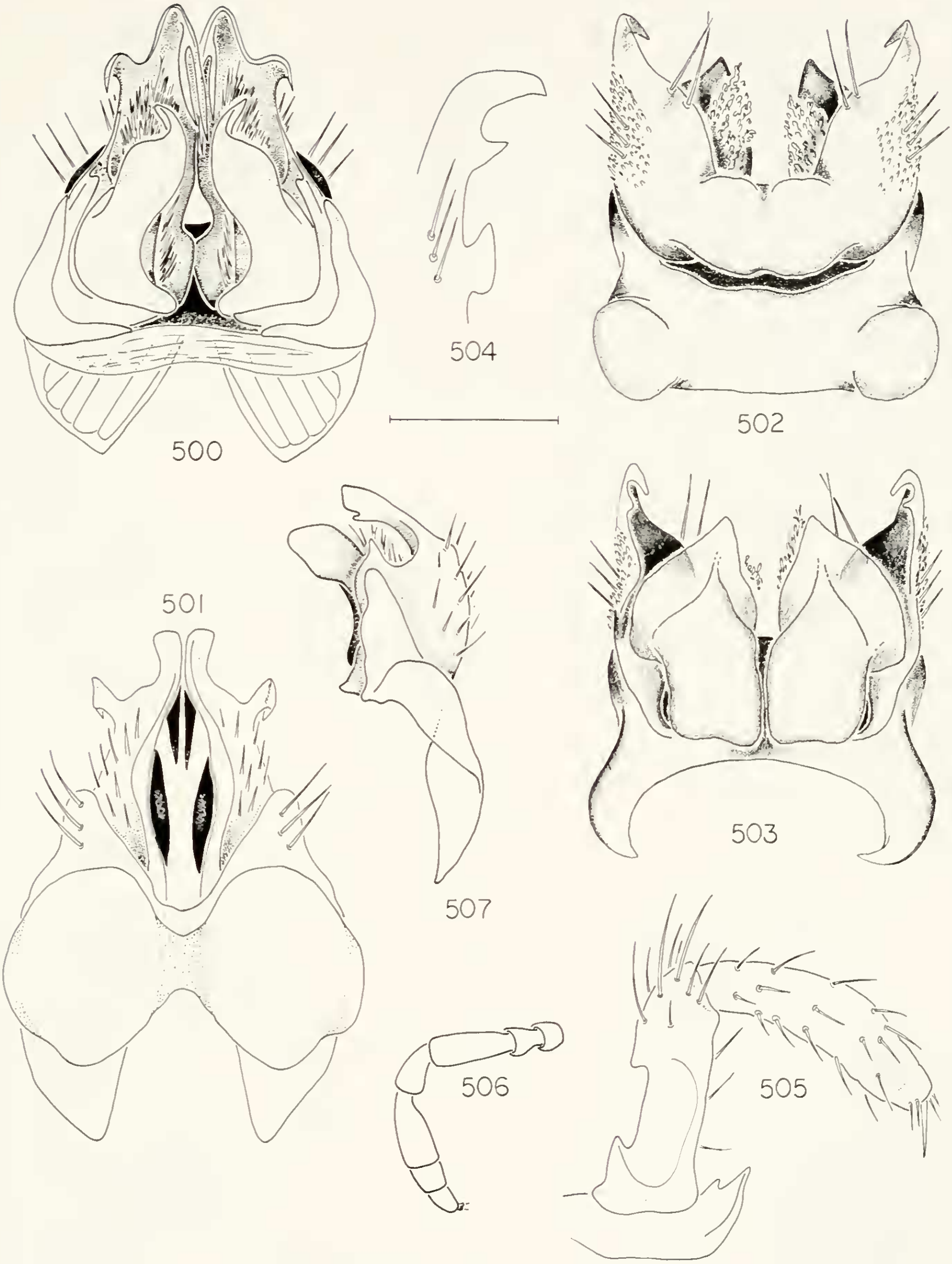
Figures 479–484. Anatomy of species of Conotylidae. Figs. 479–481. *Idagona westcotti.* Fig. 479. Gonopods, posterior view. Fig. 480. Gonopods, anterior view. Fig. 481. Right gonopods, lateral view. Figs. 482–483. *Conotyla blakei.* Fig. 482. Left anterior gonopod, posterior view. Fig. 483. Right posterior gonopod, anterior view. Fig. 484. *Conotyla albertana,* right anterior gonopod, anterior view. Scale line = 0.35 mm for Figs. 482–484; 0.50 mm for Figs. 479–481.



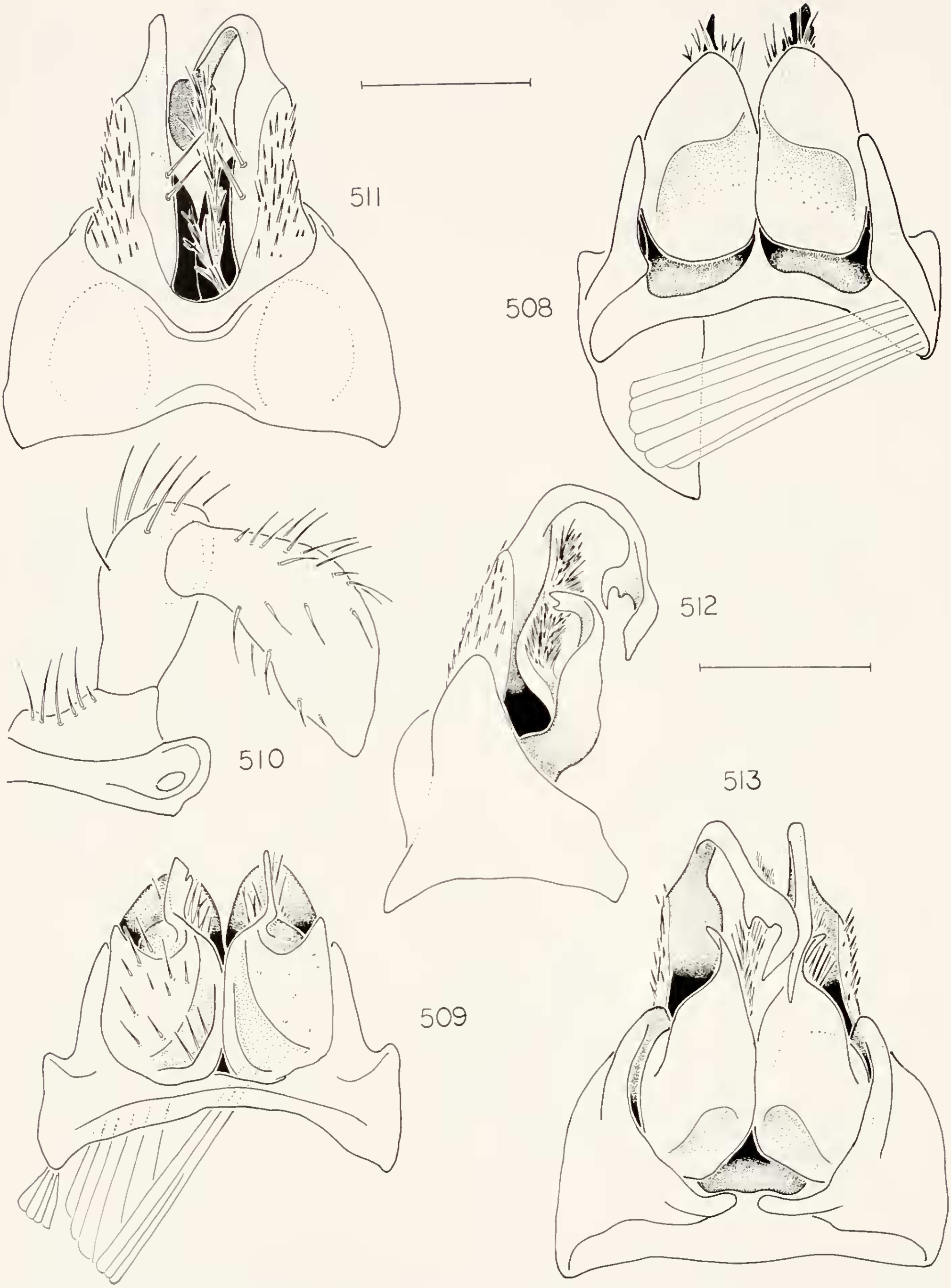
Figures 485–490. Anatomy of species of Conotylidae. Figs. 485–486. *Achemenides pectinatus*. Fig. 485. Right anterior gonopod, lateral view. Fig. 486. Right posterior gonopod, anterior view. Figs. 487–489. *Austrotyla chihuahua*. Fig. 487. Anterior gonopods, posterior view. Fig. 488. Left anterior gonopod, lateral view. Fig. 489. Right posterior gonopod, anterior view. Fig. 490. *Plumatyla humerosa*, right anterior gonopod, anterior view. Scale line = 0.35 mm.



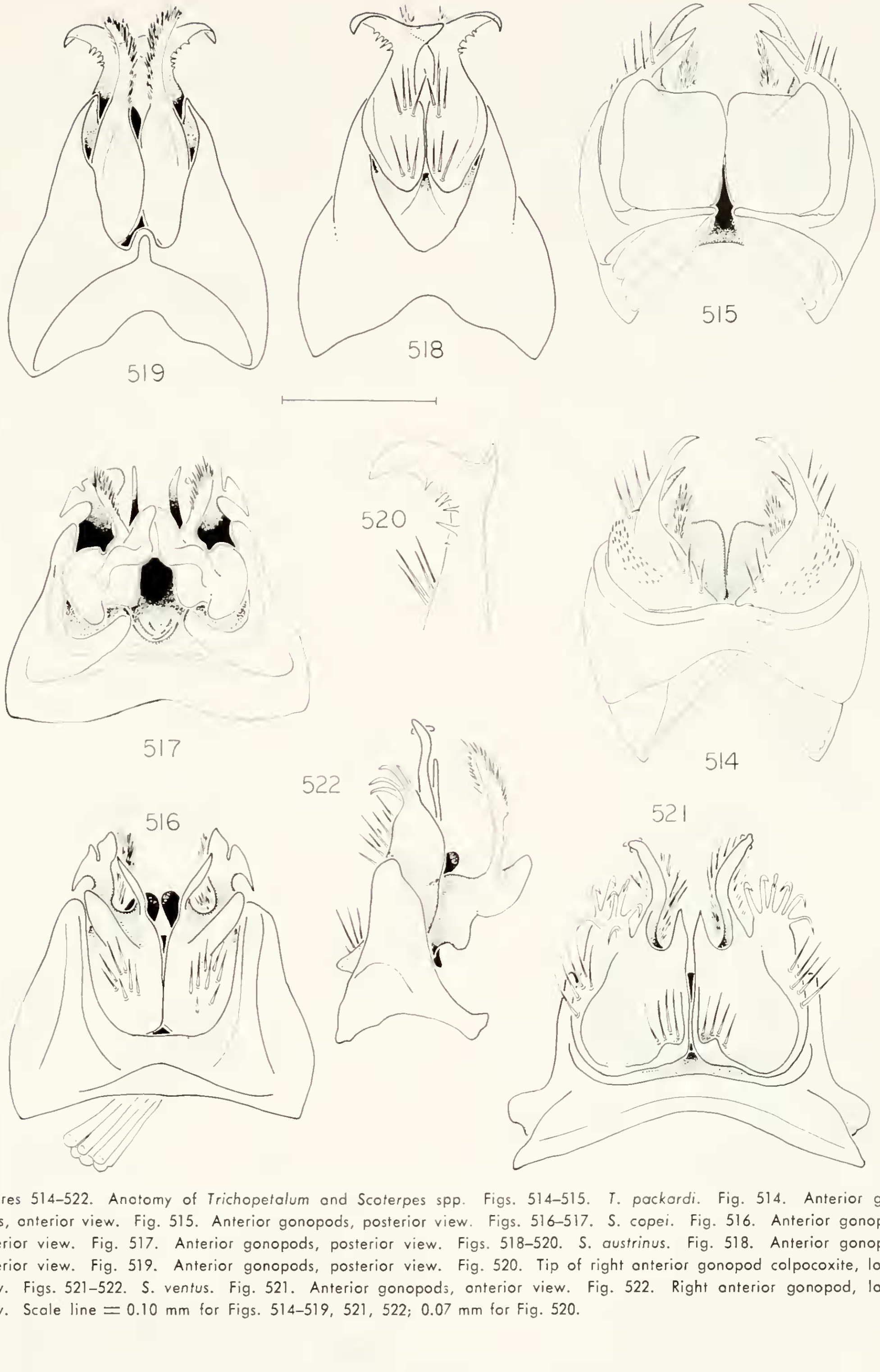
Figures 491–499. Anatomy of *Adrityla deseretae*, species of Conotylidae, and *Trichopetalum lunatum*. Fig. 491. *Plumatyla humerosa*, left posterior gonopod, posterior view. Figs. 492–493. *Taiyutyla corvallis*. Fig. 492. Anterior gonopods, posterior view. Fig. 493. Left posterior gonopod, posterior view. Figs. 494–496. *Adrityla deseretae*. Fig. 494. Right anterior gonopod, lateral view. Fig. 495. Left posterior gonopod, anteriorview. Fig. 496. Left leg 10, anterior view. Figs. 497–499. *Trichopetalum lunatum*. Fig. 497. Right anterior gonopod, lateral view. Fig. 498. Colpocoxite tip of specimen from British Columbia. Fig. 499. Colpocoxite tip of specimen from West Virginia. Scale line = 0.35 mm for Figs. 491–493; 0.60 mm for Figs. 495–496; 0.10 mm for Fig. 497; 0.05 mm for Figs. 498–499.



Figures 500–507. Anatomy of *Trichopetalum* spp. Figs. 500–501. *T. uncum*. Fig. 500. Anterior gonopods, posterior view. Fig. 501. Anterior gonopods, anterior view. Figs. 502–505. *T. dux*. Fig. 502. Anterior gonopods, anterior view. Fig. 503. Anterior gonopods, posterior view. Fig. 504. Tip of lef. anterior gonopod colpocoxite, lateral view. Fig. 505. Right posterior gonopod, anterior view. Figs. 506–507. *T. syntheticum*. Fig. 506. Right antenna, anterior view. Fig. 507. Left anterior gonopod, lateral view. Scale line = 0.10 mm for Figs. 500–503, 505, 507; 0.25 mm for Fig. 506; 0.05 mm for Fig. 504.

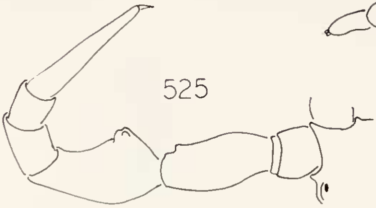


Figures 508–513. Anatomy of *Trichopetalum* spp. Figs. 508–510. *T. syntheticum.* Fig. 508. Anterior gonopods, posterior view. Fig. 509. Anterior gonopods, anterior view. Fig. 510. Right posterior gonopod, anterior view. Figs. 511–513. *T. cornutum.* Fig. 511. Anterior gonopods, anterior view. Fig. 512. Anterior gonopods, lateral view. Fig. 513. Anterior gonopods, posterior view. Scale line = 0.10 mm.

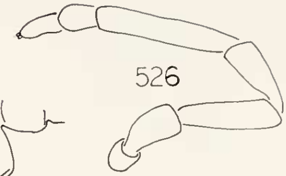


Figures 514–522. Anatomy of *Trichopetalum* and *Scoterpes* spp. Figs. 514–515. *T. packardi*. Fig. 514. Anterior gonopods, anterior view. Fig. 515. Anterior gonopods, posterior view. Figs. 516–517. *S. copei*. Fig. 516. Anterior gonopods, anterior view. Fig. 517. Anterior gonopods, posterior view. Figs. 518–520. *S. austrinus*. Fig. 518. Anterior gonopods, anterior view. Fig. 519. Anterior gonopods, posterior view. Fig. 520. Tip of right anterior gonopod colpocoxite, lateral view. Figs. 521–522. *S. ventus*. Fig. 521. Anterior gonopods, anterior view. Fig. 522. Right anterior gonopod, lateral view. Scale line = 0.10 mm for Figs. 514–519, 521, 522; 0.07 mm for Fig. 520.

523



525



526

524

527

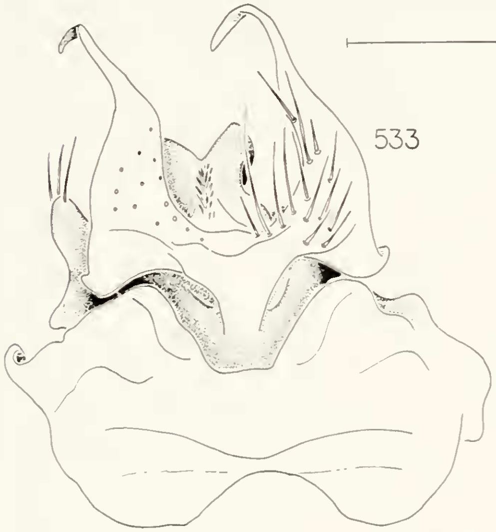
529

528

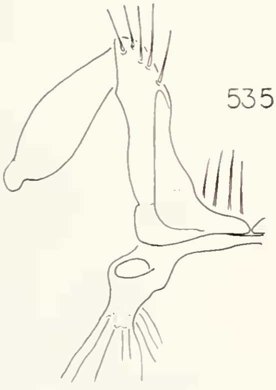
Figures 523–529. Anatomy of *Scoterpes ventus* and *Trigenotyla parca*. Figs. 523–526. *S. ventus*. Fig. 523. Anterior gonopods, posterior view. Fig. 524. Right posterior gonopod, anterior view. Fig. 525. Right leg 6, posterior view. Fig. 526. Antenna, anterior view. Figs. 527–528. *T. parca*. Fig. 527. Anterior gonopods, anterior view. Fig. 528. Anterior gonopods, posterior view. Fig. 529. *Mexiterpes sabinus*, right anterior gonopod, lateral view. Scale line = 0.10 mm for Figs. 523, 524, 527–529; 0.75 mm for Figs. 525, 526.

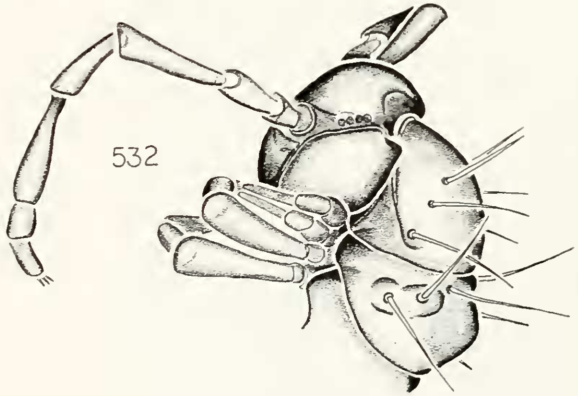

530


531

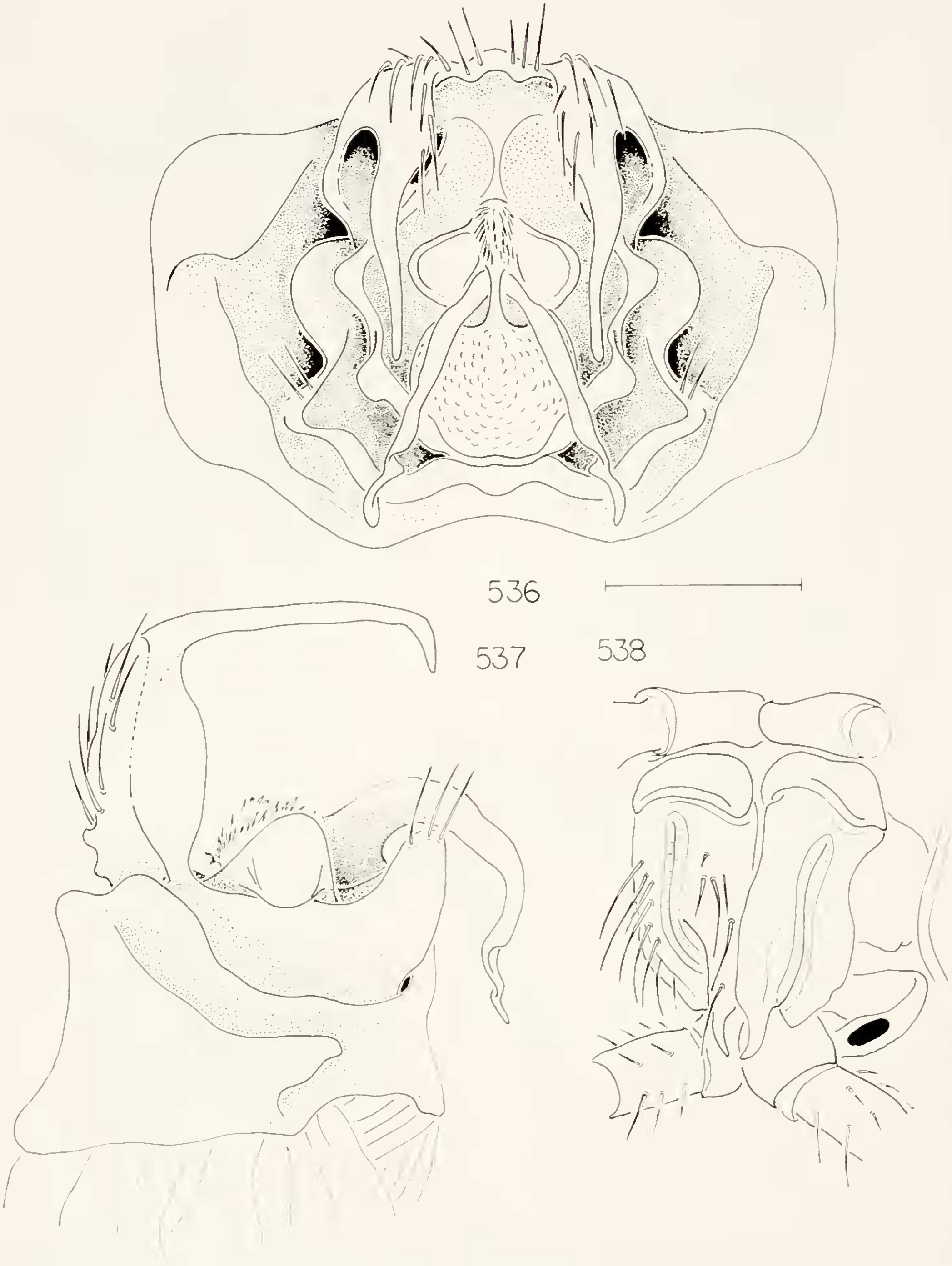

533


534


535


532

Figures 530–535. Anatomy of *Mexiterpes* spp. Figs. 530–531. *M. sabinus.* Fig. 530. Anterior gonopods, posterior view. Fig. 531. Anterior gonopods, ventral view. Figs. 532–535. *M. metallicus.* Fig. 532. Anterior end of body, lateral view. Fig. 533. Anterior gonopods, view slightly lateral of anterior. Fig. 534. Anterior gonopods, view slightly lateral of posterior. Fig. 535. Left posterior gonopod, anterior view. Scale line = 0.10 mm for Figs. 530, 531, 533–535; 0.75 mm for Fig. 532.



Figures 536–538. Anatomy of *Mexiterpes metallicus*. Fig. 536. Anterior gonopods, ventral view. Fig. 537. Anterior gonopods, lateral view. Fig. 538. Cyphopods, lateral view. Scale line = 0.10 mm for Figs. 536, 537; 0.15 mm for Fig. 538.

INDEX

Valid generic names and species combinations in italics.